National Park Service
U.S. Department of the Interior

Natural Resource Stewardship and Science

Canada Lynx Restoration at Isle Royale National Park

A Feasibility Study

Natural Resource Report NPS/ISRO/NRR—2016/1251

ON THE COVER
Photograph of Canada Lynx.
Photograph by Daniel S. Licht

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Daniel S. Licht

National Park Service
231 E. St. Joseph Street
Rapid City, SD 57701

Ron A. Moen

University of Minnesota
5013 Miller Trunk Highway
Duluth, MN 55811

Mark C. Romanski

Isle Royale National Park
800 East Lakeshore Drive
Houghton, MI 49931

Paul Brown

Isle Royale National Park
800 East Lakeshore Drive
Houghton, MI 49931

August 2016

U.S. Department of the Interior
National Park Service
Natural Resource Program Center
Fort Collins, Colorado

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Please cite this publication as:

Licht, D. S., R. A. Moen, M. C. Romanski, and P. Brown. 2016. Canada lynx restoration at Isle Royale National Park: A feasibility study. Natural Resource Report NPS/ISRO/NRR—2016/1251. National Park Service, Fort Collins, Colorado.

NPS 139/133624, August 2016

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Executive Summary

Isle Royale is a 535-km^2 island located in western Lake Superior, about 22 km from the Minnesota/Ontario shoreline. The island and surrounding islets and waters comprise Isle Royale National Park. The Canada lynx (*Lynx canadensis*) is a 7-15 kg wildcat indigenous to the boreal forests of northern North America. The species is listed as threatened in the contiguous 48 states per the Endangered Species Act. It is widely believed that Canada lynx historically occupied Isle Royale, but have been essentially absent since the 1930s. The island supports a prey base—specifically, snowshoe hare (*Lepus americanus*)—that might support a lynx population. As directed by National Park Service policies, we evaluated the ecological feasibility of reintroducing Canada lynx to Isle Royale.

Lynx were present on Isle Royale, apparently in great abundance, when explorers and settlers of European descent first reached the island. A harvest of lynx was underway by the 1890s. Reported harvests include a minimum of 48 lynx taken in the winter of 1903-04 and 67 lynx in the winter of 1916-17. We conducted a Population Viability Analysis (PVA) of the reported and assumed harvest rates from the 1890s-1930s. Although there are several possible reasons for the extirpation of lynx in the 1930s, we conclude that over-harvest was likely the primary cause. There were periodic reports of lynx on Isle Royale from the 1960-80s; however, those animals were likely immigrants from the mainland that did not persist. There is no evidence of a resident population since the 1930s.

Based on known snowshoe hare densities at Isle Royale, reported lynx densities in Minnesota and Ontario, and other scientific information we concluded that Isle Royale can support about 30 lynx on average. However, we acknowledge that the mean carrying capacity might be substantially more or less than 30 lynx due in part to the unique characteristics of Isle Royale, so we evaluated long-term viability across a range of population sizes. Furthermore, we varied the carrying capacity over time as Canada lynx populations in northern regions often go through a 10-year cycle in abundance. For example, our baseline carrying capacity of 30 lynx fluctuated from 15 to 45 animals every decade. However, some southern lynx populations show little if any cyclicity so we also evaluated non-cyclical scenarios.

We conducted a PVA of a potential lynx reintroduction to assess the persistence of the population. When we parameterized the PVA with demographic rates reported from mainland studies our cyclical model indicated a 0.36 chance of population persistence for 100 years. A non-cyclical model indicated a 0.73 probability of 100-year persistence. A sensitivity analysis of the model indicated that assumed levels of inbreeding depression had a significant impact on long-term viability. For example, when we disabled inbreeding depression the probability of persistence increased to 0.96 and 1.00 for the cyclical and non-cyclical scenarios, respectively. When we modeled the addition of 2 unrelated lynx into the population every 10 years the probability of persistence increased to $\geq$ 0.98 for both models, even when inbreeding depression was enabled. In historical times lynx might have immigrated to Isle Royale every 10 years or so via an ice-bridge connecting the mainland to the island. However, we found that the probability of ice-bridge formation in a winter has declined from 0.8 in 1959 to 0.1 in 2013, apparently due to climate change.

As a result, to mitigate for the loss of natural ice-bridge connectivity managers might have to periodically introduce new lynx to the island to avoid inbreeding depression.

However, our baseline models might underestimate lynx viability on Isle Royale because the mortality rates used in our models came from mainland lynx populations exposed to human harvest, vehicle collisions, and other anthropogenic mortality. Those mortality factors would not occur at Isle Royale. When we excluded anthropogenic mortality the 100-year persistence at Isle Royale increased to ≥ 0.99 for both the cyclical and non-cyclical models, even without augmentation and with inbreeding depression enabled. Furthermore, Isle Royale has other conditions beneficial for lynx that could not be reasonably incorporated into our models, such as the absence of competitors like coyotes (*Canis latrans*).

Conversely, climate change could deteriorate future conditions for lynx on Isle Royale. We did not parameterize climate change into our PVA due to the very speculative nature of the phenomenon; however, other studies have conducted region-wide analyses of climate change impacts on lynx and they indicate that the 100-year changes at Isle Royale would be minor. We therefore conclude that a lynx reintroduction to Isle Royale would likely be successful assuming appropriate management; however, due to the unique characteristics of the island and model uncertainties a lynx reintroduction to Isle Royale should be accompanied by a rigorous monitoring and adaptive management program.

Our PVA suggests that an initial release of 20 lynx would be most efficient as larger releases showed a negligible improvement in persistence. Released animals should come from southern Ontario as that population is not listed as threatened and the region has a similar habitat type and prey base to Isle Royale. The initial release, and subsequent augmentations should they be deemed necessary, would likely be most effective if they occurred at the ascending phase of the 10-year lynx-snowshoe hare cycle. The next such period would be around 2018-21. However, source lynx might be most available during the next population peak in Ontario, projected to be around 2021-23.

Reintroducing Canada lynx to Isle Royale appears warranted and feasible, especially if a reintroduction is accompanied with post-release monitoring and adaptive management. There would likely be little opposition to a lynx reintroduction at Isle Royale due to the protected status of the island, its isolation from development and commercial land uses, the low risk of impacts to other park resources, and the charismatic nature of Canada lynx. A reintroduction of lynx to Isle Royale would greatly contribute to our understanding of lynx ecology and conservation as the island is a unique laboratory that does not have the anthropogenic mortality factors and altered mammalian population that compromise many mainland lynx populations. As a result, Isle Royale would continue its long history and legacy of being a leader in ecological research.

Acknowledgments

We thank Rolf Peterson and other scientists who encouraged the study and provided helpful information and insight. The Great Lakes Inventory & Monitoring Program, especially Al Kirschbaum, provided critical baseline information on vegetation, pellet surveys, and other needs. Constructive reviews and input were provided by Rick Kahn and Nancy Finley of the National Park Service, Dean Beyer of the Michigan Department of Natural Resources, and Jim Zelenak of the U.S. Fish and Wildlife Service.

Introduction and Background on Isle Royale and Canada Lynx

Introduction and Justification for the Study

Isle Royale National Park, located in western Lake Superior, is world renowned for its wildlife, its wilderness character, and its scientific studies. The existing evidence suggests that Canada lynx (*Lynx canadensis*) historically occupied Isle Royale, but were extirpated in the 1930s. National Park Service policies call for restoring missing species when feasible. In addition, the Canada lynx is now listed as a threatened species and the Endangered Species Act (ESA) calls for all federal agencies, including the National Park Service, to use their authorities to restore and conserve listed species.

This study was conducted to determine the feasibility, ecological impacts, and management options of reintroducing Canada lynx to Isle Royale National Park. Because wildlife reintroductions can be costly, complex, and sometimes contentious undertakings they need to be fully evaluated using the best available science (IUCN 1995). Should the National Park Service decide to pursue a reintroduction program it will need to conduct additional analysis, specifically, appropriate planning and environmental compliance as this report primarily discusses the ecological issues of a lynx reintroduction.

Isle Royale

Introduction to Isle Royale National Park

Isle Royale National Park was authorized on March 3, 1931 and formally established on April 3, 1940, after the land was acquired. The enabling legislation stated that the:

> *"scenery, utterly distinct from anything now found in our national park system, its primitiveness, its unusual wild life and interesting flora, its evidences of possible prehistoric occupation, all combine to make Isle Royale and its neighboring islands of national park caliber."*

In October of 1976, 98% of the land in the park was designated as Wilderness (Public Law 94-567). On February 17, 1981, the park was identified as an International Biosphere Reserve. It was given such designation based on its unspoiled nature and representation of the northern forest biome.

Isle Royale National Park is comprised of Isle Royale, the largest island in Lake Superior, and the surrounding waters and other islands of the archipelago. The total area of the park is 2,313 km^2; however, only 535 km^2 are terrestrial. The main island is about 72 km long and 14 km wide at its widest point. Surrounding the main island are approximately 450 islets, also within the park boundary.

Although located at the northwest end of Lake Superior, and only about 23 km from the Minnesota shoreline (**Error! Reference source not found.**), the islands and waters actually belong to the State of Michigan (the main island is about 68 km from Michigan). The closest mainland is in Ontario, Canada, about 22 km away.

Figure 1. Isle Royale National Park is located in western Lake Superior.

The park has a relatively light history of human use and occupation. At various times prior to European settlement the islands were used by Native Americans for mining copper, fishing, hunting, and other purposes. The first immigrants of European descent arrived on the islands around the 1830s. Copper mining was active from the 1840s-1890s. Some commercial logging was done on the island; however, much of the logging was for supporting the mining operations. Eventually, almost the entire main island and many of the smaller islands were disturbed by the logging and mining operations prior to park establishment in 1940 (McLaren and Peterson 1994, Cole et al. 1997, The Nature Conservancy 1999). Unregulated trapping and hunting also had a significant impact on the park's fauna and likely extirpated some species. However, the islands still maintained much of their wilderness character. Permanent settlement of the islands essentially ended around 1940. The relicts of the mining, fishing, and logging operations, along with the archeological sites, comprise the current cultural resources at the park.

Nowadays there are no roads or year-round residents at the park. Most of the infrastructure at the park—which comprises only about 5 hectares—is for operating the park or is a cultural resource. Human use is very light at the park, with only about 15,000 visitors per year, primarily during the summer months. The park is closed to visitation from mid-fall to mid-spring. Most visitation is via ferry and seaplane from either Grand Portage, Minnesota, Copper Harbor, Michigan, or Houghton, Michigan. Many visitors stay near the two developed areas: Windigo, at the southwest end of the island, and Rock Harbor on the northeast end. The park has a network of about 265 km of backcountry hiking trails; backcountry camping is allowed in designated sites scattered throughout the park (**Error! Reference source not found.**). Other popular activities are canoeing, fishing, and wildlife watching. No wheeled vehicles (except for wheelchairs) or other mechanical forms of transportation are allowed. Hunting and trapping are prohibited; however, sport-fishing is allowed. Consistent with National Park Service policies, feeding, touching, and intentionally disturbing wildlife is prohibited. Pets are not allowed at the park, with the exception of certain employee pets and service animals where special conditions apply.

It has been stated that the park, and the nearby Minnesota mainland, are closer to a true arctic environment than any other part of the contiguous 48 states (National Park Service 2004). Most of the park is forested although small openings can be found as the result of natural processes. The forest is a mixture of northern conifers and hardwoods. Interior lakes and wetlands are numerous. For more information on the natural resources see the section: Current Natural Resource Conditions at the Park Relevant to Lynx.

The park is managed according to National Park Service policies (National Park Service 2006) and other regulations such as the Wilderness Act of 1964 and the Endangered Species Act of 1973. A General Management Plan specific to the park was completed in 1998 (National Park Service 1998). Three purpose statements were developed that are germane to this study; they are:

- Preserve and protect the park's wilderness character for use and enjoyment by present and future generations.
- Preserve and protect the park's cultural and natural resources and ecological processes.
- Provide opportunities for scientific study of ecosystem components and processes, including human influences and use, and share the findings with the public.

The park completed a fire management plan in 2004 (National Park Service 2004). The plan identified fire management objectives that included : "*allow fire to achieve its natural role in the ecosystem to perpetuate natural ecosystem processes*" and "*use prescribed fire to accomplish other specific resource management goals. These goals may include the replacement of natural fire, protection or restoration of critical plant or animal habitats or communities.*"

The park does not have any species-specific management plans in effect at this time. However, in keeping with the wilderness quality of the park the use of radio-collars and other external markings on wildlife is discouraged, but not prohibited (Oelfke et al. 2003).

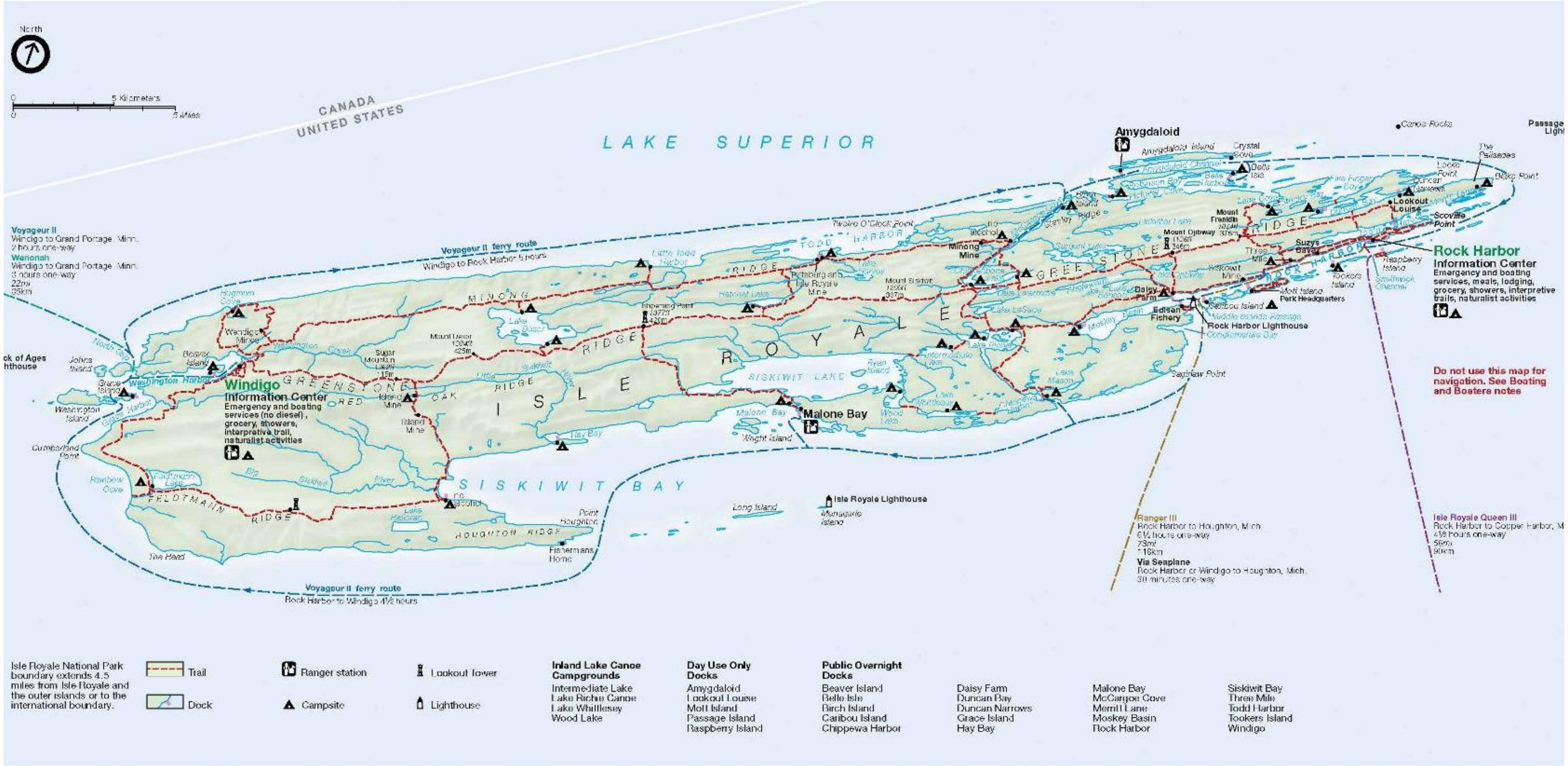

Figure 2. Map of anthropogenic features on Isle Royale.

Current Natural Resource Conditions Relevant to Lynx

The park's climate is typical of the Great Lakes Region with short cool summers (average highs 21º C) and long cold winters (average highs -3º C); however, temperature extremes at the park are attenuated by the moderating lake affect. The island's lakeshore is often cool and humid whereas the inland areas are comparatively warm and dry. Peak precipitation is June-October with mean annual precipitation of 77 cm. Mid-winter snow depths average 44 cm (Vucetich and Peterson 2011); however, snow depths have been less in recent years (R. Peterson, pers. comm.). The snow layer is generally soft; however, hard crusts occasionally form.

Ice frequently forms along the shore of the islands and sometimes forms a bridge between the main island and the mainland; with the first occurrence of > 90% ice between the island and the mainland around February 1 and the last occurrence around March 14, based on 1973-2002 ice atlases (NOAA - Great Lakes Environmental Research Laboratory 2014). However, the frequency of this condition appears to be decreasing, perhaps due to global warming. Licht et al. (2015) found that ice-bridge formation has declined from a probability of 0.8 in 1959 to 0.1 in 2013 (**Figure 3**) based on observations from the Wolf-Moose Winter Study reports (e.g.,Vucetich and Peterson 2011). They corroborated the decline with NOAA ice coverage data (**Error! Reference source not found.**) and historical ice-thickness datasets. Vucetich and Peterson (2011) reported that ice-bridges had formed in only 2 of the prior 15 years, and one of those years was the only known instance of a wolf (*Canis lupus*) immigrating to the island since the 1940s. Vucetich et al. (2012) felt that the decreasing frequency of an ice-bridge, along with increase infrastructure on the Lake Superior shoreline, has significantly reduced the likelihood of wolf immigration to the island. In February of 2015 a pair of wolves apparently crossed an ice bridge to Isle Royale, but did not stay on the island (Vucetich and Peterson 2015).

The park ecosystem is primarily boreal with vast stands of forest interspersed with numerous lakes, ponds, and marshes. Using 1997 data (The Nature Conservancy 1999), the upland areas of the park are:

37% balsam fir (*Abies balsamea*) /white spruce (*Picea glauca*)

25% aspen (*Populus tremuloides*)

18% white cedar (*Thuja occidentalis*) /black spruce (*Picea mariana*) /tamarack (*Larix laricina*) /black ash (*Fraxinus nigra*)

10% sugar maple (*Acer saccharum*) /yellow birch (*Betula alleghaniensis*)

4% sedge meadow (*Carex* sp.)

4% shrubland /barren

1% oak (*Quercus* sp.) /jack pine (*Pinus banksiana*) /white pine (*Pinus strobus*)

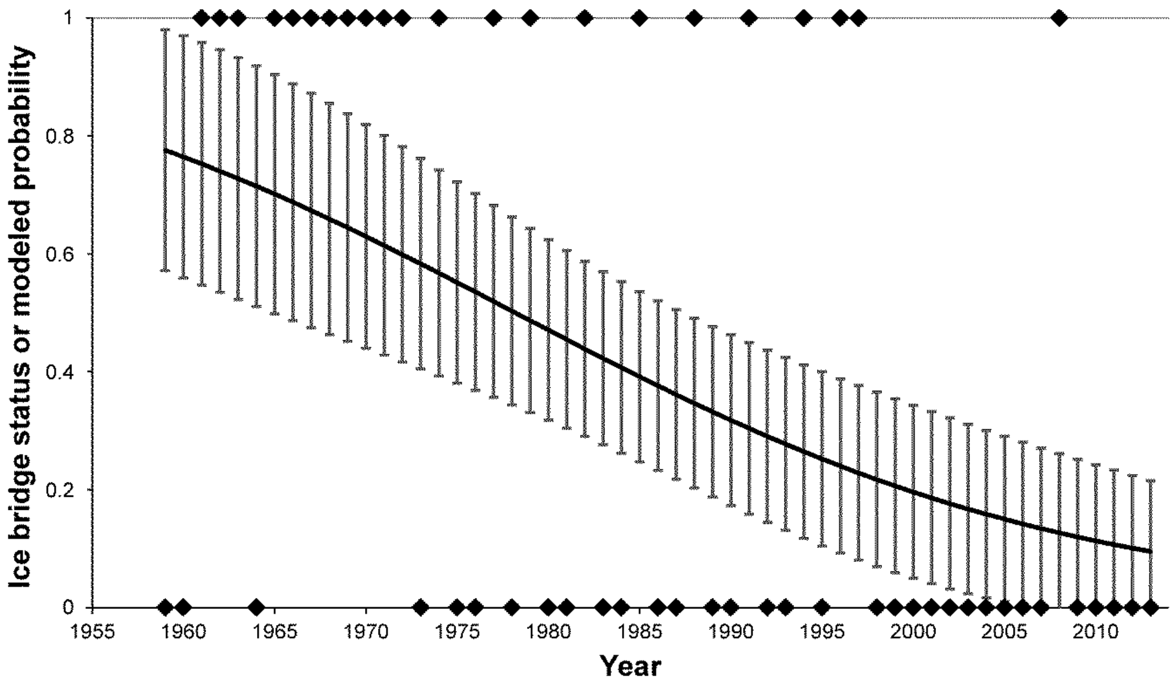

Figure 3. Observed (1=yes, 0=no) and logistic regression probability of ice-bridge formation based on visual observations (Licht et al. 2015).

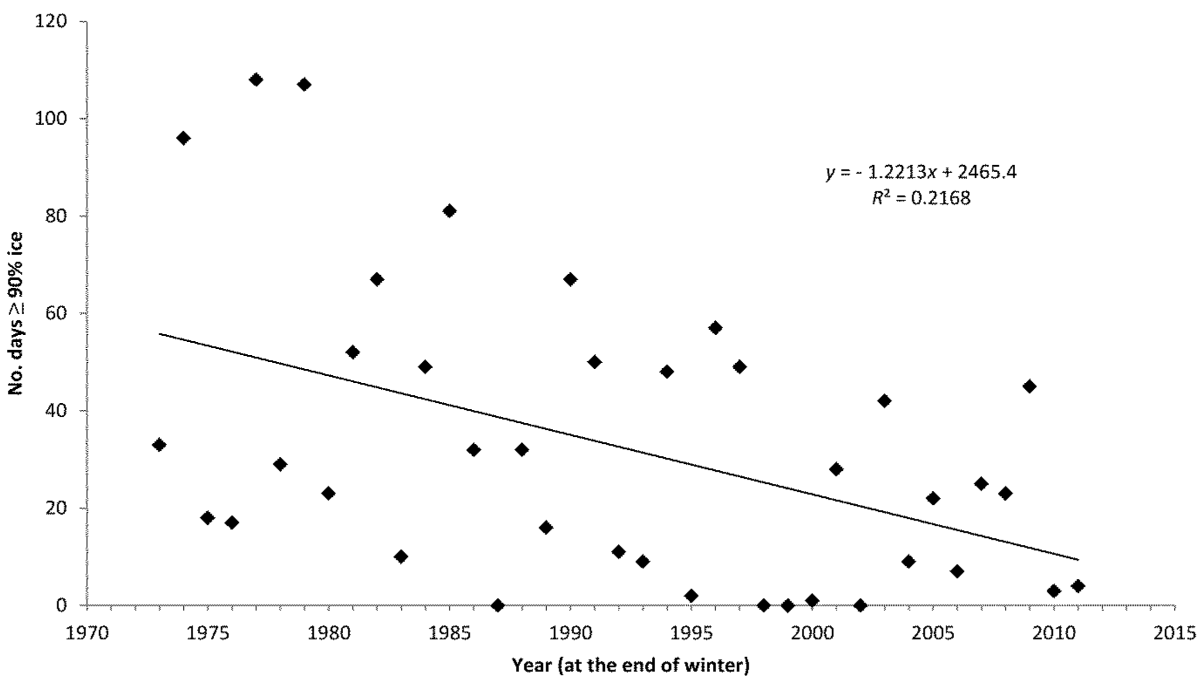

Figure 4. Frequency of an ice-bridge between the island and mainland, 1973-2002 (Licht et al. 2015).

The projected climax community in the cooler damper regions—which comprises about two-thirds of the park—is balsam fir and white spruce (**Figure 5**). The park is near the southern end of the range of this plant community, meaning the cold-adapted community could decline in the future as a result of climate change. The climax community in the warmer drier inland sites is characterized by sugar maple and yellow birch. The park is near the northern end of the range for this forest type. On the xeric ridges small stands of red oak (*Quercus rubra*), white pine, jack pine, and red maple (*Acer rubrum*) can be found. Another forest type is found in the ubiquitous swamps and bogs where black spruce, white cedar, and tamarack predominate. There are occasional openings in the forest, many due to a series of parallel ridges of exposed bedrock that run length-wise through the park. The openings support patchy grasses and shrubs such as common juniper (*Juniperus communis*). Other openings within the forest are the result of wind-throw, tree disease, fire, and herbivory (Kirschbaum and Gafvert 2013).

The forest communities are not static. For example, (Cole et al. 1997) stated that browsing by moose (*Alces alces*) is changing the composition and structure of the forest. A fire in 1936 burned about 20% of the main island; the resulting stands were comprised almost solely of paper birch (*Betula papyrifera*). However, the natural fire-frequency for the island is estimated at only 0.5-1.0 fires per year and most fires would be expected to burn slowly as is typical of boreal fires (Hansen et al. 1973). Some of the smaller islands are floristically important as they have not been altered by fire and herbivory to the degree the main island has. For a detailed description of vegetation within the park see The Nature Conservancy (1999).

The fauna community of the park is rather simple as the islands have only about half the mammal species of the mainland, but this disparity is typical of islands and consistent with the principles of island biogeography. The frigid Lake Superior waters and the vast expanse between the islands and mainland limited the number of mammals that colonized the island. For example, voles are absent from Isle Royale, but are common on the mainland.

Several species that were historically present on the island, such as the woodland caribou (*Rangifer tarandus*), Canada lynx, and coyote (*Canis latrans*) are no longer present (Mech 1966, Michigan Technological University 1985, Cochrane 1996). According to Cochrane (1996) woodland caribou and Canada lynx likely disappeared as the result of anthropogenic impacts, either directly or indirectly. The coyote likely only colonized the island following modern settlement in the region, but became extirpated shortly after wolves colonized the island around 1949 (Mech 1966, Krefting 1969). But in their short time on the island they might have contributed to the extirpation of caribou; Cochrane (1996) stated that in the late 1920s "caribou were already near extirpation (on the island) … suffering from coyote predation in addition to lynx predation."

Similar to the coyote, the red fox (*Vulpes vulpes*) appears to be a recent colonizer of the island. Cochrane (2013) stated they colonized the island around 1925. The reduction and eventual extirpation of lynx might have made red fox colonization easier as lynx are known to kill red fox (Stephenson et al. 1991, Sunde et al. 1999); perhaps because red foxes are a predator of snowshoe hares and other small mammals and therefore an exploitative competitor with lynx. It's been suggested that red fox were stocked to the island by people (http://www.nps.gov/isro/learn/nature/upload/Mammals_ver7.pdf), although others have suggested they crossed the ice (Vucetich and Peterson 2014). White-tailed deer were deliberately introduced to the island in 1910 ; however, they never took hold and none were seen after 1936 (Cochrane 1996) .

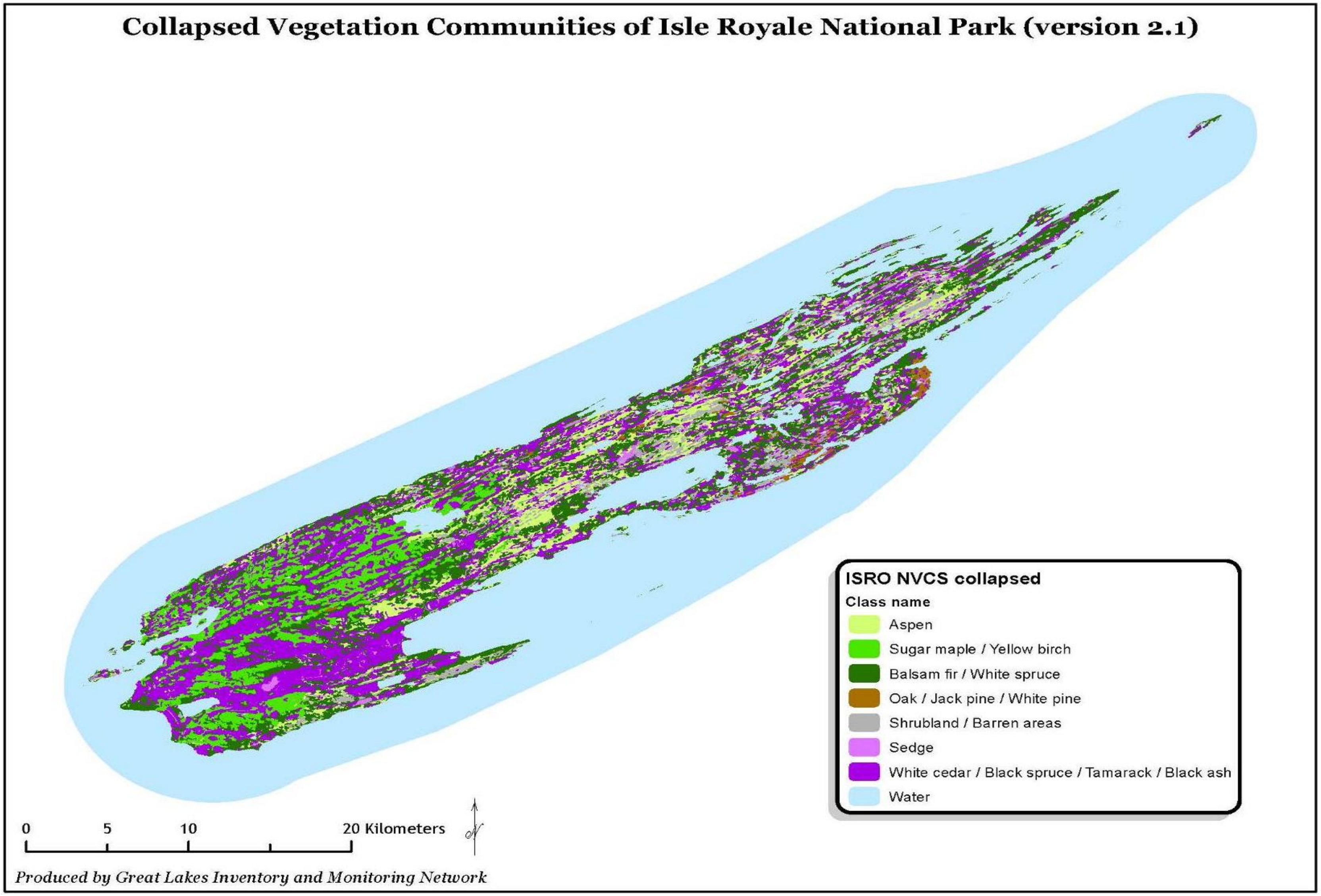

Figure 5. Vegetation communities at Isle Royale National Park.

Marten (*Martes americana*) are indigenous to the island, but have only recently been rediscovered after 60 years of no detection (Romanski and Belant 2008). The current population is likely remnant and long separated from the mainland population, based on genetic analysis (Romanski and Belant, unpub. data). Snowshoe hare can be an important prey item for marten (Cumberland et al. 2001) and might be especially important on the island as voles are lacking.

The two most famous wildlife species at the park are the wolf and the moose as the park has received worldwide fame due to a half-century of wolf and moose research. These studies are led by researchers from Michigan Technological University in what is known as the Isle Royale Wolf-Moose Study (Wolf-Moose Project 2013). However, both species might be relatively recent colonizers of the island. Palliser (1863) did not report moose or wolves as being present in 1857 nor did Adams (1909) in a 1904-05 scientific expedition. Cochrane (2013) speculated moose first arrived around 1900-1910 by human translocation, but they might have also arrived by swimming or crossing an ice-bridge. With no large predators (i.e., wolves) on the island the colonizing moose population exploded upward to an estimated 3,000 animals at which point it greatly exceeded the ecological carrying capacity of the island (Murie 1934). A severe starvation episode occurred in the early 1930s, with only a few hundred moose remaining in 1934 (Hickie 1936). A large fire in 1936 created new browse and the moose population began growing again. Cochrane (2013) concluded that wolves first colonized the island around 1948-50 and the animal(s) might have been augmented in 1951 by the release of captive animals from the Detroit Zoo. The wolf population soon increased to a couple dozen animals and separate packs were formed. On average there have been about 25 wolves and 1000 moose on the island, with both populations showing substantial variability over time. The small size of the wolf population makes it vulnerable to inbreeding, disease, and other events. For a more detailed description of the wolves and moose at the island see the numerous books and web pages devoted to the study (Mech 1966, Peterson 1995, Wolf-Moose Project 2013).

Isle Royale supports snowshoe hare, the primary prey of Canada lynx, and red squirrels (*Tamiasciurus hudsonicus*), an important secondary prey in some circumstances. The Isle Royale Wolf-Moose Study records the number of hares seen per 100 km of hiking. Although the method does not provide an estimate of hare abundance, nor is it readily comparable to most published population studies of snowshoe hares (which rely on pellet counts or mark-recapture methodology), it does provide an index of change over time. In the northern regions of North America snowshoe hare densities tend to peak every 8-11 years, generally around the turn of the decade; the Isle Royale Wolf-Moose Study hare index is consistent with that cycle with peaks occurring in 1988-89, 2000-01, and 2010-11 (Vucetich and Peterson 2011). However, the Isle Royale peaks were only about 3-4 times the long-term average suggesting attenuated amplitude compared to more northern hare populations. This reduced amplitude could be due in part to the absence of lynx on the island; however, the nearby Minnesota mainland also shows a hare cycle with less amplitude than populations in northern regions (Moen et al. 2008b). Rolf Peterson (pers. comm.) of the Isle Royale Wolf-Moose Study suggested that in the absence of lynx the hare numbers and their cycle probably reflect an interaction between weather, fox, moose, and wolf abundance, and possibly influxes of owls. However, an index of red fox abundance at the park (Vucetich and Peterson 2011) does not seem to track hare abundance to the degree that lynx populations typically do (Elton and Nicholson

1942). The Isle Royale Wolf-Moose Study hare index suggests that hares are more numerous at the northeast end of the island than they are at the southwest end (R. Peterson, pers. comm.). A very small percentage of the diet of wolves at Isle Royale is comprised of snowshoe hare (R. Peterson, pers. comm.).

Red squirrels appear to be abundant on Isle Royale (P. Brown, pers. observation). Johnson (1969) reported red squirrel densities of 2.37 and 3.63 per ha from his two study sites on the island. He also reported that the population was at or near its carrying capacity and that adult survival was high probably due to there being little predation pressure on the island. Some scholars have suggested distinct species or sub-species designation for the Isle Royale red squirrel (see Johnson 1969).

Cochrane (1996) assessed the feasibility of restoring caribou to Isle Royale and determined that the park was no longer suitable in large part because of the high wolf density at the park (1 / 100 km^2) and concerns about the availability of escape habitat. Her study suggested a 90% probability of a reintroduced caribou herd being extirpated in 40-60 years following release. There are no plans at this time to reintroduce caribou to the park.

Canada Lynx Ecology, Status, and Management

Ecology

The following is a brief overview of Canada lynx ecology, with an emphasis on characteristics relevant to a reintroduction of lynx to Isle Royale. For a more thorough discussion of lynx ecology see Ruggiero et al. (2000), Anderson and Lovallo (2003), and the Interagency Lynx Biology Team (2013). Readers should be aware that much of what is empirically known about Canada lynx is from studies in the northern part of their range and that there is comparatively less data on lynx ecology and status in the southern portion of the range (Aubrey et al. 2000, McDonald 2008, Moen et al. 2008b, Murray et al. 2008, Devineau et al. 2010). Furthermore, mainland studies report that lynx suffer high anthropogenic mortality (Mech 1980, Anderson and Lovallo 2003, Devineau et al. 2010) and therefore reported mortality rates might not be comparable to what would occur on Isle Royale.

The Canada lynx is a 7-15 kg wildcat (**Error! Reference source not found.**) found primarily in boreal habitats in Canada and the northern United States. It is similar in appearance to the bobcat (*Lynx rufus*). Notable morphological differences are that the lynx tends to be less spotted, has long black tufts on its ears, and has large feet enabling it to better walk on snow. Buskirk (2000) found that snowshoe hare and lynx have a light foot load relative to several other boreal mammals, including the red fox and wolf, suggesting that snowshoe hare and lynx are better able to move through deep soft snow (the hare foot load is lighter than the lynx, which aids it in escaping lynx in soft snow).

Canada lynx feed predominantly on snowshoe hares (**Figure 7**). When hares are abundant they can comprise almost 100% of the lynx's diet; during periods of low hare abundance they may still comprise a third of the lynx's diet (Anderson and Lovallo 2003). Anderson and Lovallo (2003) summarized 7 lynx diet studies from various regions, across all seasons (although primarily winter), and during periods of low and high hare abundance; hares were found in 79% of the samples (not weighted for sample size). Hansen and Moen (2008) found snowshoe hare in 76% of 87 lynx scats collected in the winter in Minnesota; when scats that contained only white-tailed deer were removed from the sample (deer was used as bait thereby biasing the sample), hare were found in 97% of the scats.

Figure 6. Canada lynx are generally secretive and solitary predators. Photo by Dan Licht.

Lynx kill rates of hares varies, probably in response to hare abundance, with estimates of 0.5 hares / day in Newfoundland (Saunders 1963) and 1 hare / day in Nova Scotia (Parker 1981). O'Donoghue et al. (1998) found that lynx killed 0.3 to 1.2 hares / day one year after the peak of a hare cycle in the Yukon. Saunders (1963) estimated that a lynx could consume about 170 adult hares per year, plus perhaps another 30 young animals in the summer. It's been suggested that lynx might be less tied to hare in the southern portion of the range as other prey, such as red squirrels, make up a comparatively larger portion of the diet (Roth et al. 2007a, Murray et al. 2008).

Lynx will feed on a wide variety of other prey, most notably during lows in the hare cycle and during the summer and fall months (Aubrey et al. 2000). Red squirrels (**Figure 8**) are an important secondary food source throughout the lynx's range and are especially important during lows in the hare cycle at which time they might comprise a third of the lynx's winter diet (O'Donoghue et al. 1998). Buskirk (2000) suggested that red squirrels were an important enough part of a lynx diet that squirrel habitat be considered in lynx habitat models. Lynx will also kill and eat flying squirrels (*Glaucomys sabrinus*), mice, voles, birds, and young ungulates. Lynx were significant predators of caribou calves in Newfoundland during lows in the hare cycle (Bergerud 1996). Lynx will scavenge on carrion when available. Saunders (1963) found that moose comprised 71% of the stomach volume of lynx taken in the fall in Newfoundland in an area where moose hunting was conducted. There is little information about lynx diets in the vicinity of Isle Royale, but a snow-tracking study in Minnesota reported that 24 of 26 kills were snowshoe hare; the others were a ruffed grouse (*Bonasa umbellus*) and a spruce grouse (*Falcipennis canadensis*)(Moen et al. 2008b). Regardless of the prey species, Canada lynx probably consume around 0.6 to 1.2 kg of food per day.

Figure 7. Snowshoe hare are the primary prey of Canada lynx. A healthy hare population is critical for lynx survival. Photo by Dan Licht.

Snowshoe hare populations are well known for their 8-11 year cycle. At the peak of the cycle hare abundance might be 10-25 times greater than during the lows of the cycle. These cycles are generally synchronous across large regions. The lynx population also goes through a cycle that tends to lag the hare cycle by a year or two (Elton and Nicholson 1942, Krebs et al. 2001). The cause of these cycles continues to be the subject of study and debate; with current research suggesting a complex interaction between food availability for hares and lynx predation rates. Mowat et al. (2000) suggested that the lynx decline following the peak of the hare cycle is due more to poor lynx recruitment, both in terms of pregnancy rates and kitten survival, than to adult survival.

Figure 8. Red squirrels are an important secondary prey item for lynx. When hare numbers are low red squirrels make comprise a third of the lynx's diet. Photo by Dan Licht.

It's sometimes reported that the hare-lynx cycle does not occur in the southern portion of the species' range; however, Hodges (2000) suggested that was not the case and that cycles in the southern portion have similar dynamics. She did however note that both peak and minimum hare densities were generally less in the southern portion of the species range. Based on numerous studies, including studies from the Great Lakes states, she concluded that hare populations in the southern montane and sub-boreal forests peak every 8-11 years and have amplitude of 2-25 times the minimum population.

Information on lynx survivorship, especially in non-harvested sites, is sparse. Not surprisingly, lynx survival appears to be tied to hare abundance with higher survival rates during the peak of the hare cycle. Near the peak of the hare cycle adult lynx annual survival rates tend to be around 90%; whereas at the first year of very low hare abundance adult lynx survival can be less than 40% (Poole 2003). Steury and Murray (2004) developed a quadratic equation based on published studies that showed adult survival around 95% when hare density exceeded 4 hares / ha; at hare densities less than 1 hare / ha adult survival dropped to 80%. Another of their models showed a dramatic drop in adult survival when hare density declined dramatically from the previous year. Poole (2003) summarized several studies and stated that kitten survival was high (50-83%) during the increase and peak in the hare cycle, but declined to near zero 1-2 years after hare numbers crashed. Brand and Keith (1979) found just 5-35% kitten survival during a low in the hare cycle in Alberta. Steury and Murray (2004) developed a model that showed lynx kitten survival around 70% when hare density exceeded 2 hares / ha; at hare densities less than 1.5 hares / ha kitten survival was 20% or less. Lynx survival tends to be lowest in winter, when the likelihood of starvation is highest (Poole 2003). Throughout much of the lynx range human caused mortality is significant. Moen et al. (2008b) found that about 75% of the lynx mortalities in Minnesota were due to humans. Perhaps a third to one half of the mortalities in the Colorado lynx reintroduction were due to anthropogenic causes (Devineau et al. 2010). Predation on lynx by other species has been recorded (Poole 2003). Aubrey et al. (2000) stated that both lynx survivorship and recruitment were, as a general statement, lower in the southern portion of the specie's range.

The lynx breeding season is generally in March and April. Based on placental counts, during periods with high hare densities 73-93% of adult females and 33-100% of yearlings breed (Poole 2003). The female lynx will only mate with one male each season, but the male may mate with multiple females. Gestation lasts around 64 days, so that the young are born in May or early June. Before birth, the female prepares a maternal den, usually in very thick brush and typically inside thickets of shrubs/trees or woody debris. During the increase and peak of the hare cycle adult lynx produce 4-5 kittens; during the low of the cycle lynx recruitment essentially fails (Poole 2003). Moen et al. (2008b) reported a mean litter size of 3.3 from 10 radio-collared females in Minnesota. Kittens begin hunting at between seven and nine months of age and leave the mother at around ten months, as the next breeding season begins. Males and females generally reach sexual maturity at about two years of age.

Lynx are generally solitary animals except for females with kittens and males and females during the brief breeding period. There is little overlap of home ranges within a sex; however related females seem to have more tolerance for overlap (Anderson and Lovallo 2003). Male home ranges may overlap the home ranges of multiple females. Home ranges tend to be larger during periods of low hare abundance; although site fidelity from year-to-year appears strong (Poole 2003). Home ranges of male lynx in Minnesota varied greatly from 29 to 522 km^2 and females from 5 to 95 km^2 (Burdett et al. 2007). The core areas—based on a 60% fixed-kernel isopleths—ranged from 6 to 190 km^2 for males to 1 to 19 km^2 for females. A study in the Yukon found that when hare densities dropped below 0.5 / ha that lynx home ranges dissolved and the animals became nomadic (Ward and Krebs 1985).

Juvenile animals typically disperse prior to their mother giving birth to a new litter of kittens. Dispersal distances can be several hundred kilometers. The scientific literature suggests that an increase in dispersing animals occurs when hare densities are low, although sub-adults might disperse even when hare numbers are high (Poole 2003).

Lynx densities range from < 3 / 100 km^2 to 45 / 100 km^2 during peak hare years (Slough and Mowat 1996). There is good evidence that lynx density can be tied to a single factor; that being hare density. For example, Stenseth et al. (1997) used a time-series analysis of trapping returns from northern Canada to show that lynx densities are solely regulated by prey (i.e., hare) availability. Lynx densities in the southern portion of the species range are generally around 2-3 / 100 km^2 (Poole 2003). Vashon et al. (2012) estimated a minimum lynx density in Maine of 9.2-13.0 lynx / 100 km^2. Lynx abundance in the southern portion of the species range appears to be strongly influence by lynx immigrations from further north in response to low hare populations (Murray et al. 2008).

Lynx are strongly tied to snowshoe hare and their distribution and habitat use reflects that relationship. Hodges (2000) described southern hare habitat as a forest having a well-developed understory such as is common in early seral stages, but could also occur in coniferous forests with mature trees and open over-stories. In Minnesota, lynx were found in habitats that included jack pine, balsam fir, black spruce, trembling aspen, and paper birch (Mech 1980). Moen et al. (2008b) stated that lynx in Minnesota are found in their highest densities in younger forests with a conifer understory, the same habitat where one would expect to find the highest hare densities. Burdett et al. (2007) reported that lynx in Minnesota consistently selected for 10-30 year-old successional forests, but they also used mature forests. The animals also selected for the edges between mature upland-conifer forest and successional forest. McCann (2006) found high snowshoe hare pellet densities in wetlands, coniferous forest, regenerating/young forest, and shrubby grassland in Minnesota, but did not find high densities in deciduous forest stands. Poole (2003) stated that fire and logging can create early successional habitat thereby creating optimal hare and lynx habitat; however, such processes could also reduce denning habitat. In Minnesota, female lynx with kittens tended to use den sites that contained more conifer and regenerating forest (Moen et al. 2008a). Organ et al. (2008) found that natal dens in Maine tended to be associated with blown-down trees and high visual obscurity at 5 meters from the den. Hoving et al. (2005) modeled lynx habitat in eastern North America (i.e., New York State to Nova Scotia) and concluded that high snowfall and less deciduous cover were the best predictor of lynx habitat; high conifer cover was also important in some models. They explained the lynx's preference for areas with less deciduous cover in terms of those areas having fewer red squirrels, a secondary prey source for lynx. They stated that lynx are unlikely to occur in areas with < 270 cm of snow / year; however, they speculated that snow cover was an indirect proxy for prey densities and competition with other predators. Gonzalez et al. (2007) concluded that lynx require at least four months of continuous snow coverage.

Ultimately, what defines lynx habitat is the availability of snowshoe hare (Keim et al. 2011). Linden et al. (2011) developed a landscape model that equated a hare density of 1.0 hare / h to 7 lynx / 100 km^2. Steury and Murray (2004) concluded from a model that a hare density of 1.1 to 1.8 hares / h was required for lynx persistence. Ruggiero et al. (2000) suggested that 0.5 to 1.0 hares / ha was needed for persistence. Simons-Legaard et al. (2013) found that hare density in lynx-occupied areas in Maine averaged 0.74 hares / ha: they recommended that landscapes be managed to promote densities > 0.5 hares /ha. Murray et al. (2008) suggested that at < 1.5 hares / ha lynx populations were not sustainable. If true, that helps explain why lynx populations in the southern portion of the range are less dense and their status is precarious. Murray et al. (2008) reported that spring and fall hare densities in the contiguous United States and southeastern Canada averaged 0.81 to 1.38 hares / h, respectively, and Hodges (2000) summarized the literature and reported peak hare densities in the southern portion of the range as one or two hares / ha.

Like all animals, lynx interact with other animal species in their ecosystem. For the lynx the most notable interaction is the predator-prey relationship between lynx and snowshoe hare. An adult lynx might consume 170-200 hares per year (Saunders 1963). As hare populations increase so do lynx populations (a numerical response) as does the kill rate by individual lynx (functional response), with the greatest predations rates about 1-4 years after the peak of the hare cycle (Anderson and Lovallo 2003). Lynx might consume 2-32% of the hare population (Anderson and Lovallo 2003). Studies have documented a significant increase in hare densities following the experimental removal of lynx and coyotes from an area (Krebs et al. 1995).

Little is known about population-level impacts of lynx on other species, such as red squirrels. An exception is caribou where a study in Newfoundland found that lynx were a significant predator of caribou calves, and that an experimental removal of lynx resulted in a 100% increase in calf survival (Bergerud 1971). However, the study occurred during a low in the hare cycle and might be non-typical.

There is evidence of lynx killing two other species of mid-size predators in what might be competition killings. Apps (2000) reported that 5 of 137 lynx kills during the winter in the southern Canadian Rocky Mountains were marten. Hansen and Moen (2008) found marten hair in lynx scat and evidence of a lynx kill of a marten near a trap site; however, in that case the marten was not consumed. They considered the marten remains in a lynx scat to be non-typical. Marten are dietary competitors for lynx, e.g., both animals feed on snowshoe hare. Lynx are known to kill red fox (Stephenson et al. 1991, O'Donoghue et al. 1995, Sunde et al. 1999); perhaps because red foxes are also a predator of snowshoe hares and other small mammals and are therefore an exploitative competitor with lynx.

Lynx appear to suffer from the presence of other mid-size predators, most notably, coyotes and bobcats. The impact might be both exploitative (competing for the same limited prey species) or interference (impeding access to resources and direct mortality). Coyotes are known to kill lynx

(O'Donoghue et al. 1995). Where lynx and bobcats overlap the latter tend to be slightly larger which might explain their competitive advantage. It's been long-believed that deep snow benefits lynx as it impedes access by coyotes and bobcats. However, anthropogenic features such as plowed roads and compacted snowmobile trails can negate that advantage (Buskirk 2000), although one study in western Montana found that coyote use of such anthropogenic features was minimal (Kolbe et al. 2007). Moen et al. (2008b) identified a lynx-bobcat overlap zone in Minnesota that generally extended from the town of Two Harbors just north of Duluth to the town of Ely: the area to the northeast of that line, i.e., the extreme northeastern corner of the state, was suitable lynx habitat.

Wolves are likely dominant over lynx; however, the degree and type of interaction between the two species is mostly unknown and probably negligible. The only detailed account we could find of a wolf killing a Canada lynx was by O'Donoghue et al. (1995) in the Yukon. They stated they were surprised by the unusual predation. Although the killed lynx was reported as being in good condition, many other lynx starved or were predated by other carnivores that winter. Buskirk (2000) stated that "wolves have been reported to kill lynx," but did not provide any citations or more detail. He concluded that the impact of wolves on lynx was exploitative and that the degree was "minimal." He also predicted that the colonization of wolves in the Greater Yellowstone Area, which would theoretically reduce the coyote population, would actually benefit lynx populations. Ripple et al. (2011) hypothesized that the presence of wolves would aid lynx recovery for the same reasons. At Isle Royale, wolves are an important control on moose density: following moose population troughs there has been a recovery in forage plants and an irruptions in hares (McLaren and Peterson 1994), which would benefit lynx. The only published report of wolves exerting population-level negative impacts on a species of lynx comes from Finland (Pullianinen 1965); however, that lynx (Eurasian lynx: *Lynx lynx*) is significantly larger than the Canada lynx and tends to prey on larger animals so it is probably more of a competitor with wolves for prey.

Lynx are susceptible to a variety of diseases, but there are no known cases of epizootic outbreaks. Wild et al. (2006) documented plague, a non-native bacterial (*Yersinia pestis*) disease, in lynx reintroduced to Colorado. Plague is not known on Isle Royale. Cannibalism has been documented with lynx, most frequently during periods of food scarcity when many animals are weak and malnourished. O'Donoghue et al. (1995) reported several instances of lynx killing other lynx in northern Canada. Lynx do not appear to be especially sensitive to people or human activities. In fact, most authors suggest a fair amount of tolerance by lynx toward human activities (Poole 2003).

Current Distribution and Legal Status

The Canada lynx is found in northern forests across almost all of Canada and Alaska; however, due to human activity it is no longer found in Prince Edward Island or on the mainland of Nova Scotia. In the Lower 48 states the animal is now generally restricted to the portions of Montana, Idaho, Washington, Oregon, Utah, Colorado, Minnesota, and New England.

Moen et al. (2008b) projected that northeastern Minnesota could support about 200 lynx based on habitat characteristics and a lynx density of 3 / 100 km^2. However, he noted that Minnesota is at the southern end of the species range and that "invasions" of lynx could periodically occur as a result of snowshoe hare crashes in Canada (Mech 1973, Henderson 1978). In fact, there is some question about the viability of lynx in Minnesota and whether the state is a sink population (i.e., a site that cannot maintain itself without influx of animals from outside sources). Similarly, it is unknown as to what proportion of the "Minnesota" population is the result of animals immigrating from Canada in lean hare years (U.S. Fish and Wildlife Service 2000). Moen et al. (2008b) examined several data sets and determined that Minnesota does support a resident lynx population. For example, they observed that lynx in Minnesota are often in good condition suggesting that they are not animals that had recently moved into the state from Canada due to a lack of hares up north. They also noted that reproduction does occur in Minnesota, although the recruitment numbers appear to be low.

The lynx population in Ontario, Canada appears healthy, although no population estimate is available. About 750 animals are harvested annually in the province (Poole 2003). During peaks in the Canada lynx cycle in Manitoba and Ontario some lynx emigrate southward into Minnesota (Mech 1973, Henderson 1978, Mech 1980). Conservation of lynx in the Canada/Minnesota region is complicated by the fact that the species is listed as threatened in Minnesota (under the ESA) and a furbearer that is harvested in Ontario (Moen et al. 2007).

In March of 2000 the U.S Fish and Wildlife Service published a rule that listed the Canada lynx as a *threatened* species under the Endangered Species Act in the 14 contiguous states that were part of the species historical range, including the states of Michigan and Minnesota (U.S. Fish and Wildlife Service 2000). The rule stated that the species was threatened by the inadequacy of existing regulatory mechanisms. Critical habitat was designated for the species; it includes northeastern Minnesota but does not include Isle Royale. The Endangered Species Act requires the U.S. Fish and Wildlife Service to complete a recovery plan for the lynx. No such plan is yet completed; however, an outline has been developed (http://www.fws.gov/mountain-prairie/species/mammals/lynx/recovery.htm). The outline identified northeastern Minnesota as a "core area" for lynx recovery. The outline also states that core areas are comprised of at least 1,250 km^2 of boreal forest habitat. It appears from the guidance that Isle Royale might be classified as a "peripheral" area for lynx recovery.

The State of Michigan lists the Canada lynx as an endangered species in the state. The State of Minnesota lists the lynx as a furbearer with season that has been closed since 1983. The species is regionally listed in Canada, specifically in parts of Newfoundland and Nova Scotia (Mackinnon and Kennedy 2008). Ontario has a harvest season that typically runs from late October to late February

Management Practices

Lynx management generally consists of; 1) providing habitat for snowshoe hares, 2) protecting large tracts of wilderness with minimal roads and access, 3) reintroducing lynx to vacant habitat, and 4) managing lynx harvests. As a result of the lynx's threatened status in the contiguous 48 states, the latter is only relevant in Canada and Alaska.

Habitat management for lynx typically consists of creating habitat that can support high densities of snowshoe hares. Ideal hare habitat generally consists of a ground layer high in forbs for hare foraging during the spring-fall months and high in seedlings and shrubs for foraging in the winter months. Such habitat can be created on a large scale by fire, logging, or insect infestation. However, Fuller et al. (2007) found that when stem densities are extremely high (> 14,000 ha) that lynx find the areas difficult to access and thereby use them comparatively less, even though hare densities might be greatest in such habitats. At a smaller scale events such as wind-throw and tree disease might also create the structural diversity that benefits hare populations. Although the focus of lynx habitat is on providing snowshoe hares, Buskirk (2000) recommended development of a habitat model that also includes standing mature forest that supports red squirrels. He felt that a diverse habitat that includes both early successional habitat for hares and late successional habitat for squirrels is also more likely to have the blow-downs and other structure that provides lynx den sites and shelter from inclement weather.

Another much-discussed management practice for lynx is to minimize roads, snowmobile trails, and other unnatural means of access into lynx range. Such roads and trails can increase lynx mortality via poaching, roadkills, and other anthropogenic causes. They can also lead to ingress and colonization by coyotes and bobcats, species that appear to compete with lynx. With this in mind, federal land managers in parts of the Intermountain West restrict snowmobile use in lynx habitat because the compacted trails created by the machines provide easy access for coyotes (Bunnell et al. 2006). Such trails could also increase access by bobcats which could lead to an increase in bobcat-lynx hybridization (Schwartz et al. 2004, Homyack et al. 2008).

The Lynx Conservation and Assessment Strategy (LCAS: Ruediger et al. 2000) identified risks to lynx conservation in North America:

Table 1. Risks to lynx in North America.

Affecting Lynx Productivity	Affecting Lynx Survival	Affecting Lynx Movements
Timber Management	Trapping	Highways, Railroads, Utility Corridors
Wildland Fire Management	Predator Control	Land Ownership Pattern
Recreation	Shooting	Ski Areas and Resorts
Backcountry Roads and Trails	Competition and Predation Influenced by Humans	
Livestock Grazing	Highways	
Human Developments		

Fortunately, none of these risk factors are known to occur at Isle Royale National Park or are expected to occur, with the exception of wildland fire management and backcountry trails. However, backcountry trails at Isle Royale are only used during the summer months and therefore should not be an issue at the park. The list is informative in that it shows some of the advantages of Isle Royale for lynx.

Although lynx can move great distances (Mech 1973), including across treeless areas (Adams 1963), landscape fragmentation might prevent lynx from re-colonizing parts of their historical range. Therefore, wildlife managers have twice used reintroductions in an attempt to re-establish lynx populations. From 1989-1991, 83 lynx were translocated from the Yukon to the Adirondack

Mountains in New York State. Many of the animals dispersed great distances and mortality was high, including significant mortality due to vehicle collisions (Kloor 1999). Within 2 years nearly half the individuals had died. Despite considerable searching since the releases, no animals are known to exist from that effort (Aubrey et al. 2000).

Starting in 1997, the Colorado Division of Wildlife began a program to reintroduce lynx from animals captured in Canada and Alaska (Devineau et al. 2010, Colorado Division of Wildlife 2011, Devineau et al. 2011). From 1999-2006 the program released 218 wild-caught lynx. Although lynx survival was relatively low in the early years, and starvation occurred (Kloor 1999), survivorship and recruitment increased and the program is now considered a success (Devineau et al. 2010). Some of the animals wandered widely from the core area, as far away as Iowa, northern Idaho, and eastern Nevada. Mortality of dispersing animals was 1.6 times that of animals that stayed on the reintroduction site (Devineau et al. 2010). The reintroduction effort found that holding lynx in captivity at the reintroduction site for several weeks and feeding them well dramatically improved their monthly survival over the first year after their release (Devineau et al. 2011). The release protocol ultimately adopted by the program called for coinciding the release with annual snow melt in late March or April. Based on a model, Steury and Murray (2004) concluded that “reintroduction success was associated with number of release events, total number of animals released, and time of the release relative to the phase of the hare cycle.”

Unfortunately, there appears to be few sites in the contiguous United States that hold promise for lynx recovery. Steury and Murray (2004) wrote “successful lynx reintroduction requires high hare densities and minimal anthropogenic disturbance; few areas in the contiguous USA currently possess such qualities.” Isle Royale National Park has minimal anthropogenic disturbance; however, what is uncertain is whether the hare population on the island can support a viable lynx population. Furthermore, the small size of the island might make a reintroduced lynx population vulnerable to inbreeding depression and stochastic events.

Study Objectives

This feasibility study has the following four objectives:

1. Document the historical status of lynx and the cause of the extirpation.
2. Assess the feasibility of long-term survival of a reintroduced lynx population.
3. Recommend reintroduction and other management actions, if a reintroduction is feasible.
4. Discuss the potential impact of a lynx reintroduction on the park ecosystem and park management.

Methods

Following is a summary of the methods used for this study.

Methods Used to Determine the Historical Status and Causes of the Extirpation

To document the historical status of lynx at the park and the possible reasons for their disappearance we searched the published and unpublished literature, reviewed databases, and consulted with people who have knowledge of the subject. Whenever possible and appropriate, references are provided. As part of the database review we searched the National Park Service NPSpecies database (http://science.nature.nps.gov/im/apps/npspp/index.cfm). This database includes a list of records of plant and vertebrate species known to occur at a park. Significant effort went into populating this database. We also conducted a search of museums in an effort to locate voucher specimens from Isle Royale. The search included the MaNIS network (http://manisnet.org), a database network which includes catalogues from Michigan State University, the University of Michigan, the University of Minnesota, and the Royal Ontario Museum.

We reviewed all plausible explanations for the extirpation of lynx at Isle Royale. Over-harvest was suggested as the cause by several authors; therefore, we developed and conducted a simulation model that imposed historical harvest rates on plausible lynx populations in the early 20th century. The methods and analysis are captured in Licht et al. (2015). This report summarizes that paper, and expands on it in some places.

Methods Used to Assess the Current Lynx Carrying Capacity

Potential carrying capacity is a critical information need in evaluating the feasibility of animal reintroductions. This study used several methods to assess the current lynx carrying capacity at Isle Royale.

Historical Records. We reviewed historical records for evidence of the lynx carrying capacity of Isle Royale. This review included records of the number of animals harvested.

Lynx Home Ranges and Densities on the Mainland. A second approach to evaluate the lynx carrying capacity of Isle Royale is to look at the land area of the island and project how many lynx it could support based on lynx home ranges and densities for similar habitats on the mainland. Male lynx are generally territorial with little overlap in the core area of their home ranges; females overlap with male ranges and on occasion with other females. For this analysis we used lynx home range size and population densities from Minnesota and western Ontario.

Vegetation Types. Another approach to evaluating lynx carrying capacity is to correlate existing vegetation types to known hare abundance for such types. Hare abundance can then be used to estimate lynx abundance as there is a strong correlation between the two (see Anderson and Lovallo 2003). Vegetation types for Isle Royale National Park were mapped in 1997 (The Nature Conservancy 1999). Moen et al. (2008b) developed a relationship between vegetation types and hare densities in Minnesota. We cross-walked island vegetation to the hare densities that they reported for similar vegetation on the Minnesota mainland. We then used the formula of 1.0 hare / h to 7 lynx / 100 km^2 (Linden et al. 2011) and multiplied that by the size of the island to estimate a carrying capacity.

Hare Densities. A more direct way to estimate hare densities at a site is to conduct pellet surveys as there is a strong correlation between pellet density and hare abundance (Krebs et al. 2001, McCann et al. 2007, Berg and Gese 2010). Once a hare density is estimated it can be converted to a lynx density using the ratio of 1.0 hare / h to 7 lynx / 100 km^2 (Linden et al. 2011). In 2011-12 pellet surveys were conducted at Isle Royale by Ron Moen and Mark Romanski using the method of McCann et al. (2007). Surveys were stratified by habitat type and the results weighted for area. We also used historical pellet counts collected by Peter Jordan.

Methods Used to Assess Long-term Viability and Management Options

The International Union for the Conservation of Nature recommends that a population viability analysis (PVA) be conducted to evaluate the probability of a success of a wildlife reintroduction and to compare management alternatives (IUCN 1995). To conduct such an analysis we used the program VORTEX (Miller and Lacy 2005, Lacy and Pollak 2014). The model requires user inputs for variables such as survival, reproduction, carrying capacity, and immigration. To parameterize the model we relied heavily on the comprehensive review by Anderson and Lovallo (2003), values from Minnesota (Moen et al. 2008b) and other lynx studies in the southern portion of the species range (e.g., Vashon et al. 2007), and other studies and models (e.g., Steury and Murray 2004). More information on the mechanics and assumptions of the model can be found in Licht et al. (accepted). The key parameters are listed below showing the mid-point value and the variability during the 10-year cycle, where appropriate:

Percent females breeding: 25 ± 25 for yearlings and 95 ± 5 for adults

% of Males in breeding pool: 75

Lethal Equivalents: 6.29

Age of first offspring for females: 2

Age of first offspring for males: 2

Maximum age reproduction: 10

Maximum number of broods per year: 1

Maximum number of young per litter: 6

Young per litter: 1.8 ± 1.7 for yearlings and 3.3 ± 1.2 for adults

Sex ratio of young: 50:50

Kitten (age 0-1) mortality for both sexes: 60 ± 30

Yearling (age 1-2) mortality for both sexes: 25 ± 20

Adult mortality for both sexes: 10 ± 10 over 10-year cycle

Catastrophes: 0

Carry Capacity: 30 ± 15 over 10-year cycle

The VORTEX model used by Licht et al. (accepted) to assess the viability of a reintroduced lynx population was also used to design and test various management scenarios including initial reintroduction size and the timing, and the frequency and size of supplementations. The results of those simulations provide the basis for management recommendations. We also relied on the scientific literature, the advice of experts, and lessons learned from the New York and Colorado reintroductions. The reintroduction recommendations presented here are only general. Specific actions would have to be developed by the park, some of which would be part of an environmental compliance and restoration plan.

Results

Historical Status and Possible Reasons for the Extirpation

Historical Status

To better understand the historical status of lynx at Isle Royale we evaluated all of the information we could find. Much of the following chronological list was developed in 1998 by M. Romanski of Isle Royale National Park (unpub. rep.).

- 300 BC to 500 AD – Lynx bone fragments were reported from an archeological site at Indian Point (Cleland 1966). The site was most likely used in the summer months (Cleland 1968).
- 1400 AD or later – Lynx remains were reported from a site at Isle Royale (Cleland 1966).
- 1857 – The Palliser Expedition landed on Isle Royale on June 12, 1857. Palliser's report on the expedition states "the lynx is the largest animal on the island, and is said to be very common" (Palliser 1863).
- 1890 – W.P. Scott, a resident of the Wendigo mine settlement, noted the presence of lynx (Martin 1988).
- 1897 – Martin (1988) stated that "commercial exploitation of lynxes was underway on the island by 1897."
- 1897 – C.L. Raymond, in written accounts of a fishing trip, observed "Mr. Johns, Jr., had four wildcats, which he had trapped, chained to stakes, awaiting orders from Lincoln Park, Chicago, for shipment to its zoological department" (Martin 1988).
- 1903-04 – C.C. Adams (Adams 1909) stated that "Victor Anderson and son, John, secured 48 (lynx) skins during the winter of 1903 and 1904. Most of these were from about three miles southeast of the head of Rock Harbor, in the vicinity of Lake Richie." Martin (1988) stated that the harvest suggests an island population >100 individuals.
- 1904 – Edwards Island residents killed a lynx with an oar that was swimming from their island. Based on a photograph the animal appeared to be a juvenile (Martin 1988).
- 1904-1905 – Five lynx were taken for the University of Michigan Museum of Zoology collection (Martin 1988).
- 1904-1905 – C.C. Adams (Adams 1909), lead a University of Michigan expedition that documented the natural resources of the island in the summer of 1904 and 1905

Figure 9. Lynx killed in 1904 when swimming between islands. Photo from NPS archives.

(primarily the latter). Noteworthy quotes include “Hares had been numerous, as was shown by the large amount of excrement, and there similar evidence of the occurrence of Lynx” (15), “the body of a Lynx was found hanging on a tree where it had been left by a trapper” (30), “Squirrels were exceedingly abundant” (399), “with the possible exception of the White-footed Mouse, the Hare is the most abundant mammal upon Isle Royale … their distribution was quite general” (410), and, “the Lynx apparently wanders about over much of the island and seems to frequent in particular the rocky ridges, at least the tracks were especially abundant in such places … the Hare and Red Squirrels furnish and abundance of food for them” (414).

- 1917 – An anonymous article in the Daily Mining Gazette reported that the Michigan Department of Conservation offered bounties for predators which brought a succession of trappers to Isle Royale. W.H. ‘Ping’ Foster, Sam Bennet, and Paul Opitz overwintered in 1916-1917 and reportedly set traps for coyote, lynx, mink, red fox and marten.
- 1916-17 – W.H. Foster wrote that 67 lynx were captured on the island in 1916-17 (Foster 1917).
- 1917-18 – D. Snyder, in personal communication in 1987, stated that Holger Johnson and Otto Olson live-trapped lynx in the winter of 1917-1918 (Martin 1988).
- 1925, 1927 – E. Cochrun, in his biennial report for the Michigan Department of Conservation, told of Bill Lively, an employee of the Department and the best known Isle Royale trapper, who resided at Hay Bay in the 1920's. Lively trapped at least 119 coyotes in just four winters on the island. Although no lynx figures were given, Milford Johnson recalled that Lively indeed trapped lynx during the mid-1920's (Mech 1966, Martin 1988).
- 1926 – W.P.F. Ferguson, commenting on the cyclical nature of hare-lynx populations, wrote that on Isle Royale "the lynx died off from starvation one winter when there were no rabbits" (Martin 1988).
- 1926 – F.M. Warren, an island resident, wrote "a few years ago there were numerous lynx, which have now almost entirely disappeared, caught by trappers who spent several winters on the island" (Martin 1988).
- 1928-29 – P.F. Hickie, in a 1943 report for the Michigan Department of Conservation, stated that three trappers were employed with the Department during the 1928-1929 trapping season.
- 1930s – J. Zerbey of the National Park Service wrote that “in the early 1930’s the Michigan Conservation Office trapped over 25 lynx” (cited in Mech 1966). Martin (1988) noted that this was during a period when regional lynx populations were at record low levels.
- 1960s-70s – Johnsson et al. (1982) reported that there were sightings of a “cat” in various seasons during the 1960’s and 1970’s, but did not provide details.

- 1963 – Cochrane (1996) cited sources and wrote “evidence of natural immigration included credible lynx sightings in 1963, 1970, 1981, and 1988; each being a year when regional populations were on the rise and irruptive migrations were recorded on the mainland.”
- 1965 – Glen Merrit, an island resident, in an oral interview with L. Rakestraw, commented that lynx were once "quite numerous" and later asserted that lynx remained present until roughly the 1930's (Mech 1966, Martin 1988).
- 1963 – Johnsson and Shelton (1964) report that NPS employees observed either a lynx or bobcat in May of 1963.
- 1966 – L D. Mech wrote that the J. Zerbey report of lynx being trapped in the early 1930s is “the last record of the species on Isle Royale (Mech 1966).
- 1970 – On March 8 the Isle Royale Wolf-Moose Study pilot Don Murray and park ranger Zeb McKinney saw a cat on the ice of Lake Richie. According to Murray the cat had long tufts on the ears (R. Peterson, pers. comm.). As reported in (Johnson et al. 1970), “Later (Durwood) Allen and Murray examined and measured the tracks and decided it was a lynx. This confirms occasional summer reports of cat observations over the past several years.”
- 1970 – Cochrane (1996) cited sources and wrote “evidence of natural immigration included credible lynx sightings in 1963, 1970, 1981, and 1988; each being a year when regional populations were on the rise and irruptive migrations were recorded on the mainland.”
- 1977 – Peterson (1977) listed the lynx as “currently present” in a monograph on wolf ecology at Isle Royale; however, he stated that he did not observe any animals and that “if lynx are still present on the island, they are very rare.”
- 1979 – Baker (1983) reported a sighting in 1979, but provided no supporting details.
- 1980 – Mark Cramer of the Isle Royale Wolf-Moose Study had a cat snarl at him from close range (R. Peterson, pers. comm.). This observation was just a few days after an observation by a park employee of a cat on the shore of Tobin Harbor (R. Peterson, pers. comm.). (Note that (Martin 1988) reported on what might be the same observation, but he attributed it to the “summer of 1981.”)
- 1981 – Cochrane (1996) cited sources and wrote “evidence of natural immigration included credible lynx sightings in 1963, 1970, 1981, and 1988; each being a year when regional populations were on the rise and irruptive migrations were recorded on the mainland.”
- 1988 – Cochrane (1996) cited sources and wrote “evidence of natural immigration included credible lynx sightings in 1963, 1970, 1981, and 1988; each being a year when regional populations were on the rise and irruptive migrations were recorded on the mainland.”
- 1988 – Martin (1988) reviewed the history of lynx at Isle Royale and assessed the habitat and concluded that a “lynx reintroduction is a readily justifiable option … Isle Royale might

support 10-50 individuals … however, it perhaps should not be given high management priority … there is reason to anticipate the natural recolonization of Isle Royale by dispersal across the ice from northwestern Ontario or northeastern Minnesota."

- 2000 – In the rule listing the lynx as a threatened species it stated that: lynx persisted on Isle Royale in Lake Superior into the late 1970s (U.S. Fish and Wildlife Service 2000).

A query of the MaNIS database (http://www.manisnet.org) on September 16, 2011 did not find any lynx records from Isle Royale National Park. There were records of 10 lynx specimens from the Michigan State University catalogue and one from the University of Michigan, but only two animals were from Michigan (1960 and 1962) and the rest were from Canada. A search of the Royal Ontario Museum returned 10 records, but none were reported from Isle Royale. McKelvey (2000) also conducted a review of historical lynx records; he documented the 1904-05 trapping of five lynx on Isle Royale by the University of Michigan, but did not list any other records from the island.

Based on the available information it appears that a viable lynx population existed on Isle Royale until the 1930s. It appears that a few individuals occasionally immigrated to the island from the mainland from the 1960s-1980s; however, it seems implausible that a breeding population persisted on the island for the entirety of those years. Although Isle Royale is remote, accessibility is low, and the cover is thick, the island has been the site of exhaustive research by the Wolf-Moose Study and others. Much of the field work for that study occurs in winter when lynx tracts would be very recognizable. It is very unlikely that a self-sustaining lynx population could have persisted all those years without regular observations and evidence by the researchers and others.

Reasons for the Extirpation

Understanding the reasons for the disappearance of lynx from Isle Royale is paramount to determining whether a reintroduction should take place. If the causes of the extirpation are still present then it's unlikely that a reintroduction would be successful. There are numerous possible explanations for the disappearance of Canada lynx from Isle Royale National Park. Of these, one seems most plausible as a primary explanation; however, others may have contributed to the decline. The following evaluation and discussion summarizes the findings of Licht et al. (2015).

Disease: Licht et al. (2015) reviewed the historical and scientific literature for diseases that might have caused or contributed to the lynx extirpation in the 1930s. They found no evidence that disease played a factor in the extirpation of lynx from Isle Royale.

Systemic Transitional Changes in the Vegetation Community: The vegetation community on Isle Royale has changed dramatically in the past century due primarily to logging, fire, and moose overabundance (Murie 1934, Mech 1966, Snyder and Janke 1976). Licht et al. (2015) concluded that systemic changes in habitat at Isle Royale—primarily related to moose over-abundance—might have contributed to the extirpation of Lynx on the island. However, they found no evidence that habitat changes were the sole or primary cause of the lynx extirpation.

Changing Mammal Community: Coyotes appear to have colonized Isle Royale by 1912 (Krefting 1969). They are widely believed to be significant competitors of lynx (Buskirk 2000). Cochrane

(1996) and Cochrane (2013) stated that red fox colonized the island in the 20th century; they could have competed with lynx for snowshoe hare and other small prey. Licht et al. (2015) concluded that the changing mammalian community, especially the presence of coyotes, might have been a stress on the lynx population at Isle Royale, but they did not conclude that the changing mammalian community was the sole or primary cause of the lynx extirpation.

Cyclical collapse in prey populations: The interacting temporal population dynamics of Canada lynx and snowshoe hare are well known (Elton and Nicholson 1942, O'Donoghue et al. 2010). When hare populations' crash they are typically followed by a lynx population crash. Historical and current evidence suggests that Isle Royale's hare population does oscillate (Martin 1988, Allen 1994, Vucetich and Peterson 2011). Therefore, lynx could have been extirpated due to a prey population collapse. However, Licht et al. (2015) concluded that a cyclical collapse in prey populations was not the sole or primary cause of the lynx extirpation at Isle Royale. They based their conclusions in part of the fact that lynx remains were found at Isle Royale from pre-Columbian times, the species was abundant when the first people of European descent visited the island around 1850, and lynx were common up to the 1930s, suggesting that the lynx population persisted on Isle Royale through numerous hare cycles. Furthermore, the island has a red squirrel population that might have provided an important alternate prey for lynx during periods of hare shortage (Roth et al. 2007b, Murray et al. 2008).

Over-harvest: The historical record from Isle Royale includes harvests of 48 lynx in the winter of 1903-04, 67 lynx in the winter of 1916-17, and over 25 lynx in the 1930s (Adams 1909, Foster 1917, Mech 1966, Martin 1988). These are likely minimum harvests. For example, the report of 48 lynx captured in 1903-04 was by a father-son combination and primarily from a small portion of the island (Adams 1909). Licht et al. (2015) assumed a peak carrying capacity of 75 lynx on Isle Royale and modeled the historical rates of harvest. They found that over-harvest alone could have caused the extirpation and that over-harvest was likely the primary reason for the extirpation of lynx from Isle Royale. This conclusion had been suggested by others (Mech 1966, Johnsson et al. 1982, Martin 1988), but not quantitatively supported.

Decreasing Ice-bridge Formation: In their model simulations of the historical lynx population on Isle Royale, and the role of harvest in the extirpation of the population, Licht et al. (2015), found that decreasing rates of ice-bridge formation between the mainland and the island could have played a role in the lynx disappearance. Based on their simulations, historical lynx populations on Isle Royale needed periodic immigrants to prevent inbreeding depression. Immigration could have only occurred across ice-bridges between the mainland and the island. However, they found that ice-bridge formation has declined dramatically since the 1960s both in terms of frequency and duration (Licht et al. 2015). The decline might have started as far back as the 1900s (Licht et al. 2015). Therefore, decreasing ice-bridge formation might have retarded genetic and demographic augmentation in the existing population, thereby contributing to the extirpation. Yet decreasing ice-bridge formation cannot explain the rapid demise of the population. However, decreasing rates of ice-bridge formation might have precluded natural lynx recolonization on the island since the 1930s.

We believe that over-harvest was the primary reason, and perhaps the sole reason, that lynx were extirpated from Isle Royale in the 1930s. Hence, a lynx reintroduction appears ecologically feasible as harvest has been prohibited on the island since Isle Royale National Park was established in 1940. Even illegal harvest is a negligible concern due to the remoteness and wilderness character of the island. Therefore, a reintroduction appears appropriate per National Park Service policies (National Park Service 2006). Yet special considerations and management actions might be necessary to mitigate for other changes to the island, most specifically, in regards to changes in ice-bridge formation.

Current Carrying Capacity

Several methods, some quantitative and some based on best professional judgement, were used to estimate how many lynx Isle Royale can support. Together, these methods provide the best estimate of current lynx carrying capacity on the island.

Historical Records

There are no known historical surveys or estimates of the size of the historical lynx population on Isle Royale. However, there are historical harvest records that could be used to infer the size of the population. Regrettably, there are large temporal gaps in the harvest records, suggesting that perhaps only the most noteworthy harvests were recorded. Furthermore, some of the historical harvests might have consisted in part of lynx that crossed an ice-bridge to the island during lynx irruptions in Canada (i.e., the harvests included non-resident as well as resident animals). Despite these concerns, we evaluated the historical harvest record for purposes of determining how many lynx Isle Royale might have supported.

In the winter of 1903-04, Victor Anderson and his son secured 48 skins from the island. Most of these were reported as being from “the vicinity of Lake Richie” suggesting they harvested a relatively small portion of the island’s lynx population. Based on historical lynx harvest records from Canada (Poole 2003), the Canada population was at that time just a few years past a nadir so the harvest was probably not augmented by recent immigrants from the mainland.

In the winter of 1916-17, 67 lynx were captured on the island. There is no evidence that this harvest extirpated the population. At this time the lynx population cycle in Canada appeared to be in the decline phase (Poole 2003). Therefore, it’s plausible that the Isle Royale population, and the harvest, had been supplemented by recent immigrants from Canada.

The only other substantial harvest information that provides clues on the lynx carrying capacity for the island is a record of “over 25 lynx” being trapped in the “early 1930’s.” Because the time period for this record is not specific it does not provide the snapshot of the population that the other records do. Furthermore, it cannot be compared to the lynx population cycle in Canada. It is noteworthy that the 1930’s were a time of severe moose overabundance on the island and that coyotes, a competitor and predator of lynx, were well established.

Based on these records it appears that Isle Royale was historically able to support substantially more than 67 lynx, at least for short periods of time. Even during a low in the lynx cycle in Canada—a period when immigration to Isle Royale was less likely—the island still supported at least 48 lynx during one winter. Licht et al. (2015) assumed that Isle Royale historically supported 75 lynx for purposes of their baseline model, but they also ran simulations at 38 and 113 lynx. Martin (1988) suggested that the island historically supported >100 lynx based on the rates of historical harvests. A historical carrying capacity of >100 lynx seems plausible and perhaps likely; however, the habitat on Isle Royale has changed substantially since lynx occupied the island so estimates of historical carrying capacity might not be applicable to the current situation.

Lynx Home Range and Densities on the Mainland

A second approach for evaluating the lynx carrying capacity of Isle Royale is to look at the land area of the island and project how many lynx it could support based on reported lynx home range sizes and densities for similar habitats.

In assessing the potential maximum lynx occupancy of Voyageurs National Park in northern Minnesota, Moen and Windels (2009) used a home range core area of 50 km^2 for male lynx and 25 km^2 for female lynx. The figures came from lynx telemetry studies in the Superior National Forest in northern Minnesota. Using those values, Isle Royale could support a maximum of 11 males and 22 females, or 33 lynx total.

Poole (2003) stated that the few published studies in southern boreal forests suggest relatively static lynx densities of 2-3 animals per 100 km^2. Similarly, Moen et al. (2008b) used a density of 3 lynx per 100 km^2 when estimating the size of the Minnesota lynx population. Using the figure of 3 lynx per 100 km^2 Isle Royale could support 16 lynx.

However, it is widely reported that lynx home ranges and densities are a function of hare abundance (Anderson and Lovallo 2003). Therefore, if hare abundance on the island differs from these mainland areas then the island's lynx carrying capacity should also differ.

Vegetation Types

Another approach for estimating the lynx carrying capacity at the island is to compare the island's vegetation to other areas where there is a known correlation between vegetation types and hare abundance. Hare abundance can then be used to estimate lynx abundance as there is a strong correlation between the two (Anderson and Lovallo 2003). Moen et al. (2008b) developed a relationship between vegetation types and hare densities in Minnesota that can be used to estimate hare abundance on the island. Vegetation types for Isle Royale National Park were mapped in 1997 (The Nature Conservancy 1999) and those types were cross-walked to vegetation types on the Minnesota mainland (**Table 2**).

Table 2. Vegetation types on Isle Royale and hare densities from comparable types on the mainland.

Habitat Type on Isle Royale	Hectares on the Island	Minnesota Equivalent	Hares / ha in Minnesota	Estimated Hare Population
Balsam Fir / White Spruce	20,002	Upland Conifer	0.34	6,800
Aspen	13,450	Deciduous	0.03	403
White Cedar / Black Spruce / Tamarack / Black Ash	9,827	Lowland Conifer	0.16	1,572
Sugar Maple / Yellow Birch	5,158	Deciduous	0.03	154
Sedge	2,247	Wet Fen	0.72	1,617
Shrubland / Barren	2,157	Shrubby Grassland	0.47	1,013
Oak / Jack Pine / White Pine	598	Mixed Forest	0.19	113
Total	**53,439**			**11,672**

Based on this analysis, the weighted density of hares / ha for the island is 0.2, which extrapolates to a carrying capacity of 8 Canada Lynx. This hare density is well below most density estimates in the southern portion of the specie's range (Murray et al. 2008) and well below what some perceived as the minimum hare density necessary to sustain lynx (Steury and Murray 2004). However, a better analysis of hare density on the island can be made by conducting pellet surveys of hare abundance.

Hare Densities

An effective way to estimate hare densities is to survey hare pellets, typically by counting pellets within a 1 m^2 plot, and then using a known relationship between pellet counts and hare abundance (McCann 2006). Peter Jordan has conducted hare pellet surveys on the island since 1984. In 2011 Ron Moen led a relatively more intensive survey for purposes of this feasibility study. Using those surveys, and the formula developed by Linden et al. (2011), the projected lynx carrying capacity on Isle Royale has ranged from 19 to 42 across 4 decades (**Table 3**).

Table 3. Snowshoe hare pellet surveys on Isle Royale and conversion to projected lynx abundance.

Parameter	Jordan 1980's	Jordan 1990's	Jordan 2000's	Moen 2011
Mean pellets / m^2 weighted by habitat type	1.44	0.82	1.23	1.81
Correlated to hares / hectare	0.9	0.5	0.8	1.1
Correlated to lynx carrying capacity	34	19	30	42

Other Considerations

Many estimates of lynx densities and lynx carrying capacity are from areas where lynx are exposed to anthropogenic mortality factors, degraded and fragmented habitats, and altered mammalian communities. For example, lynx in nearby Minnesota and Ontario are subjected to illegal and legal (Ontario only) harvests, collisions with vehicles, and competition with coyotes and bobcats. As a result, lynx survival and therefore lynx densities could possibly be lower at these mainland sites then it will be at Isle Royale where the impacts are not present. However, quantifying how these habitat differences will translate to differences in carrying capacity is difficult and speculative, in part because there are no places in the southern lynx range that have the unique characteristics of Isle Royale. It's possible that mainland mortality factors are compensatory and that mainland lynx densities would be no higher even if these factors were not present. While we believe that Isle Royale might have a relatively higher carrying capacity than the mainland, we cannot quantify the difference. However, we do quantitatively account for anthropogenic mortality in some of our PVA simulations of persistence (see below).

Estimated Lynx Carrying Capacity at Isle Royale

In conclusion, we believe that the 2011 survey by Moen, which extrapolates to a carrying capacity of 42 lynx, is the best estimate of how many lynx the island can support. However, that survey was likely during a peak in the hare cycle. Therefore, we believe that a more conservative estimate of 30 lynx is appropriate for planning a reintroduction of lynx to Isle Royale. The number of lynx might range from 15 at lows in the hare cycle up to 45 lynx near the peak. Those figures were used by Licht et al. (accepted) to assess the long-term viability of a reintroduced lynx population to Isle Royale. But we recognize that the long-term mean lynx carrying capacity at Isle Royale could be substantially less or more than 30 lynx so we assess the viability of other population levels as well.

Population Viability Assessment

Licht et al. (accepted) used the software program VORTEX to run a variety of simulations assessing the viability of a reintroduced lynx population and the effect of various management options. This section summarizes those findings. More detailed information can be found in Licht et al. (accepted).

They found that a lynx population reintroduced to Isle Royale has a 0.36 probability of persistence for 100 years, assuming a carrying capacity of 30 lynx cycling from 15 to 45 animals every 10 years (**Table 4**). A non-cyclical population has a 0.73 probability of persistence. Inbreeding depression had a severe effect on population persistence in the models. When they disabled inbreeding depression the probability of persistence increased to 0.96 for the cyclical model. Historically, the lynx population on Isle Royale probably avoided inbreeding depression via lynx immigrating across an ice-bridge from the mainland (Licht et al. 2015). Licht et al. (accepted) found that just adding 1 male and 1 female every 10 years increased the probability of persistence to ≥ 0.98 in the models. They also stated that their baseline models might underestimate lynx persistence on Isle Royale because they were parameterized with demographic rates from mainland studies, most of which were exposed to harvests and vehicle-caused mortalities. When they excluded assumed rates of anthropogenic mortality the probability of 100-year persistence was ≥ 0.99 for the cyclic and non-cyclic models, even without immigration.

Licht et al. (accepted) then evaluated a variety of management options. They found that supplementing lynx to Isle Royale during the ascending phase of the lynx cycle was most effective. Supplementing lynx during the peak or nadir of the cycle was moderately effective whereas supplementing lynx during the declining phase was less effective. This was because those animals released at the low of the cycle had lower likelihood of surviving and contributing their genes to the resident population. (Licht et al. accepted) then tested a variety of supplementation sizes and frequencies using the cyclic model. The simulations suggest that the population had a high probability of persisting for centuries, and even millennia, with frequent supplementations and that even less-frequent supplementations should keep the population viable for the foreseeable future (**Figure 10**). Furthermore, when they conducted sensitivity tests on their model they found that supplementations maintained the population across a wide range of plausible demographic rates, i.e., even in worse case scenarios.

Table 4. Probability of 100-year lynx persistence under various scenarios.

Scenario	Probability of Persistence	Mean Years and SD to Extinction	Final Expected Heterozygosity	Final Number of Alleles
Cyclical (baseline model)	0.36	71 ± 19	0.40	2.3
Non-cyclical	0.73	77 ± 17	0.45	2.7
Cyclical: without inbreeding depression	0.96	52 ± 28	0.47	2.9
Cyclical: augment 2 lynx every 10 years	0.98	61 ± 26	0.85	11.5
Cyclical: excluding anthropogenic mortality	0.99	63 ± 27	0.57	3.8

Licht et al. (accepted) found that initial release sizes of 20 to 50 lynx had a 100-year probability of persistence of 0.31-0.36 whereas an initial releases of 4 and 10 lynx had probabilities of 0.07 and 0.25, respectively, in the cyclic model without supplementation. They concluded that the supplementation schedule was much more important at conserving lynx than was the initial population size.

Licht et al. (accepted) acknowledged there were many uncertainties in their models, which is one reason why they conducted and presented a range of simulations. They also conducted sensitivity analyses. A one-factor sensitivity tests holds all parameters constant except for the parameter of interest. That parameter is varied and simulations conducted. The analysis helps to better understand uncertainty and key parameters in population persistence. **Figure 11** shows how varying the values of parameters used in the lynx model affects the probability of persistence. For example, a rate of 6.29 lethal equivalents was used to model inbreeding depression, resulting in a probability of persistence of 0.36 in the baseline cyclical model. That rate is the default rate in VORTEX version 10; however, version 9 of VORTEX used a default rate of 3.14 lethal equivalents. If 3.14 had been used in the lynx baseline cyclical model the probability of 100-year persistence would have been about 0.80 (**Figure 11**). Similarly, if the long-term carrying capacity is only 15 lynx (with the population oscillating from an average of 7.5 to 22.5 over the 10-year cycle) the probability of 100-year persistence is essentially zero. The analysis shows that adult and kitten mortality rate, lethal equivalents, and carrying capacity were very influential in determining population persistence.

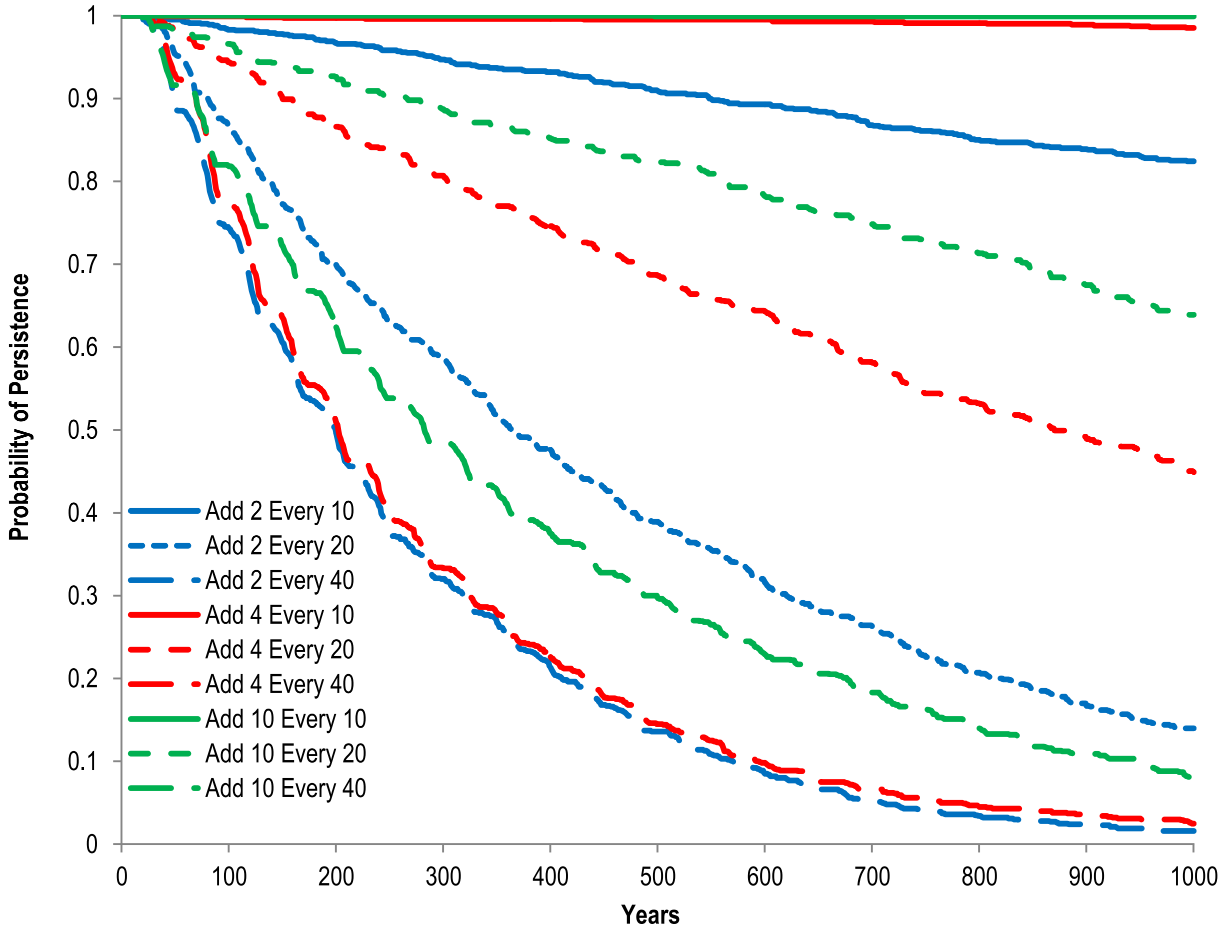

Figure 10. Probability of persistence under various supplementation schedules for the baseline cyclical model (expanded from Licht et al. accepted).

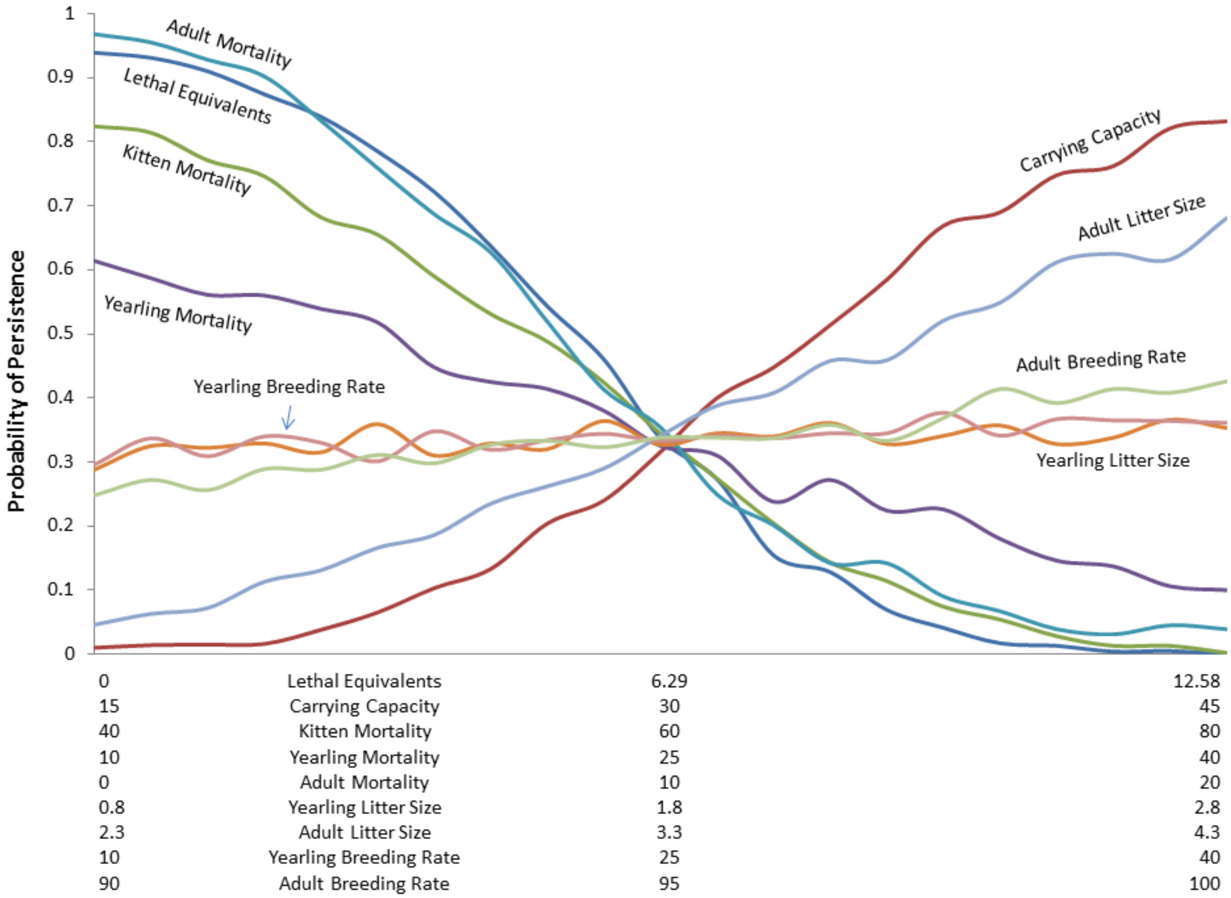

Figure 11. Spider plot of cyclical model sensitivity test (revised from Licht et al. accepted).

The sensitivity analysis can be used to better understand management options. For example, the supplementation of 2 lynx ever 10 years resulted in a relatively high probability of persistence regardless of carrying capacity. Even if the carrying capacity is only 15 lynx a regular supplement of 2 animals every 10 tears increases the probability of 100-year persistence to of 0.91. In fact, supplementation of 2 lynx every 10 years increases the probability of 100-year persistence to above 0.90 across a range of plausible values for the parameters in the model (**Figure 12**).

A Latin hypercube sensitivity test varies multiple parameters (e.g., carrying capacity, lethal equivalents, and mortality rates) simultaneously and randomly. Licht et al. (accepted) conducted a Latin hypercube test of the lynx model and the capability of supplementations to overcome or mitigate for model uncertainty. When they added 2 lynx every 10 years at the ascending phase of the cycle 95% of the sensitivity test scenarios had > 0.50 probability of 100-year persistence. In other words, supplementation can overcome all but the worst-case scenarios (e.g., high mortality, low reproduction, and low carrying capacity all at the same time).

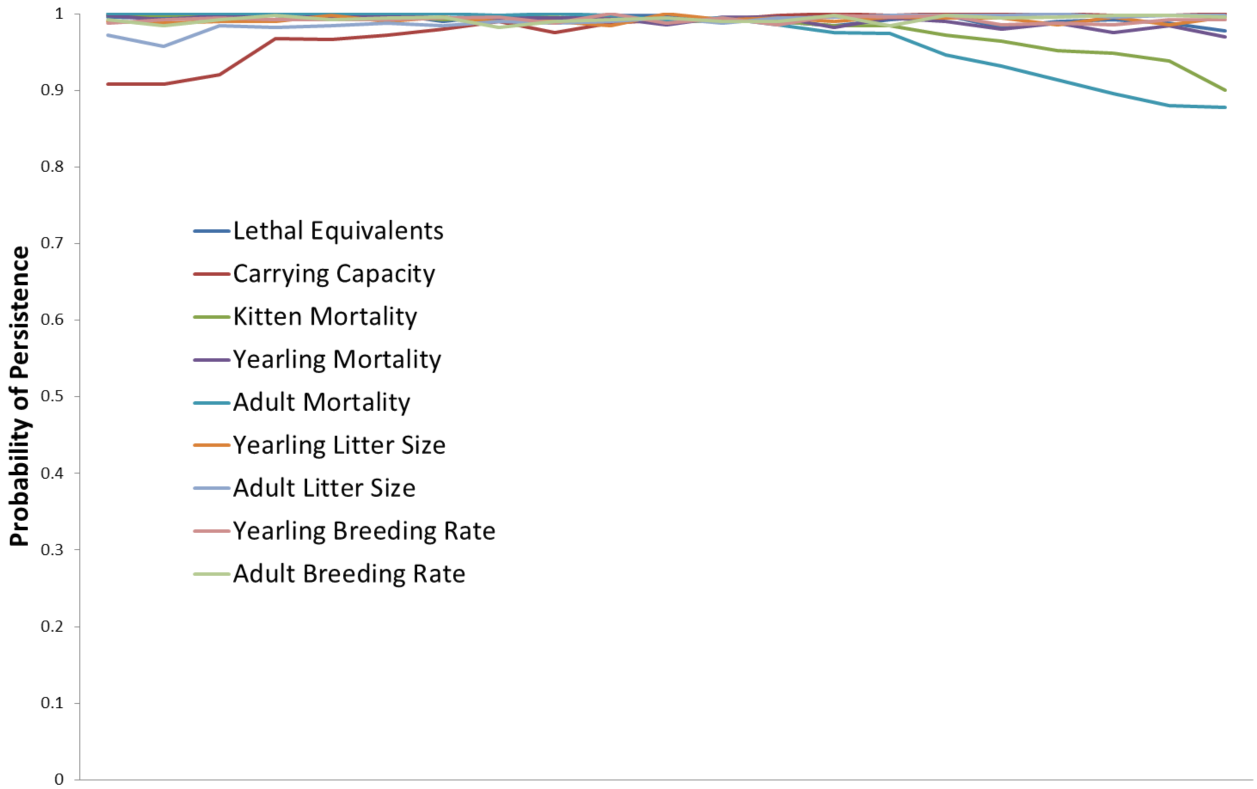

Figure 12. Same analysis as Figure 11 but adding 2 lynx to the population every 10 years.

Discussion and Summary

Isle Royale National Park is famous for its wild denizens. Yet ironically, the two most celebrated occupants, the wolf and the moose, appear to be recent colonizers to the island (Cochrane 2013). And both have, arguably, thrown the island into a state of flux, perhaps to the detriment of ecosystem integrity and several indigenous species. Cochrane (1996) wrote:

> *Ironically, the only "natural" system that has been proven to work on Isle Royale, by surviving for more than 3,500 years of prehistory, is a caribou-lynx-snowshoe hare-Native American community.*

Of those three wildlife species, only the snowshoe hare still occupies the island. Cochrane rejected the idea of restoring caribou due in part to the changes over the past hundred years, including the colonization of the island by wolves.

In contrast, restoration of Canada lynx appears feasible, especially with appropriate monitoring and management. All wildlife reintroductions are fraught with uncertainties, and restoring lynx to Isle Royale is no exception. Partly as a result of those uncertainties we conducted and presented a range of analyses and simulations. From those, readers and decision-makers can make informed decisions based on their comfort level. We believe there is a very high likelihood of reintroduction success. Although our baseline cyclical model showed relatively poor success, it was explained by assumed inbreeding rates and easily mitigated by the periodic introduction of new lynx. Furthermore, a simulation model that excludes assumed levels of anthropogenic mortality—which would not be present on Isle Royale—gives a 0.99 probability of success for 100 years. The lack of anthropogenic factors at Isle Royale appears to be an advantage over the reintroduction site in Colorado (Devineau et al. 2010), an effort that is now considered a success. Even if Isle Royale Canada lynx experience the same demographic rates as mainland populations, the island population should remain viable assuming immigration of just a few animals every decade or so. The new animals would bring new genetics into the population and lessen the risk of inbreeding depression. Such immigration can come naturally by mainland lynx crossing an ice-bridge to the island, as ice-bridges do still form in some years. For example, two wolves crossed an ice-bridge to Isle Royale in 2015, but subsequently returned to the mainland (Vucetich and Peterson 2015). If natural immigration does not occur managers might have to mitigate for the declining rate of ice-bridge formation by periodically bringing in new animals.

Climate Change

Isle Royale lies near the interface of southern deciduous and northern boreal forests so it might be especially sensitive to climate change (Sanders and Grochowski 2013). However, the moderating effect of Lake Superior could attenuate some climate-induced changes at Isle Royale, such as changes in snow amounts and conditions.

Gonzalez et al. (2007) evaluated the potential impacts of climate change on lynx conservation areas in North America. They found that lynx habitat in the Lower 48 states could decrease from one-half to two-thirds by 2100 and that lynx habitat might shift northward by as much as 200 km in some areas. However, they also found that the Superior National Forest region in northeast Minnesota—the U.S. mainland area closest to Isle Royale—would provide one of the few refuges for the species in the Lower 48. Furthermore, they show that Ontario mainland closest to Isle Royale would also continue to provide suitable lynx habitat in the future. They did not explicitly report on changes at Isle Royale, but their maps appear to show that the probability of an Isle Royale winter having suitable snow for lynx would decline from 0.95 in 1961-90 to 0.90 in 2100, suggesting that climate change would have only a minor impact on Isle Royale's ability to support lynx in the future.

Hoving et al. (2005) modeled lynx occurrences in the Eastern United States. They found that snowfall was positively correlated with lynx detections. However, they concluded that snowfall did not have a direct effect on lynx populations, but rather, high amounts of snowfall reduced competition between lynx and other predators such as bobcats and coyotes. Neither of those competitors are currently present on Isle Royale so island lynx should be more resilient to declining snowfall amounts than would mainland lynx.

We do not believe that climate change scenarios for Isle Royale are compelling or worrisome enough to preclude a lynx reintroduction to the island. It appears that Isle Royale has suitable habitat for supporting a Canada lynx population for the foreseeable future, assuming the agency is willing to take necessary monitoring and management actions. We strongly recommend that a reintroduction program be accompanied by a strong research and monitoring program due to the reintroduction uncertainties and because of the valuable lessons that could be learned. Fortunately, the park has a long history of ecological monitoring and research. A lynx reintroduction could enhance our understanding of the island's ecology.

Recommendations

Wildlife reintroductions are typically complex, costly, and uncertain affairs. Managers should expect that to hold true for a reintroduction of Canada lynx to Isle Royale National Park. Careful planning and adherence to science can improve reintroduction success and efficiency. However, administrative considerations, funding, logistics, and other factors might dictate or influence many actions. Should the National Park Service pursue a Canada lynx reintroduction to Isle Royale an environmental compliance document will be developed and specific action items identified. Our general recommendations for a reintroduction of Canada lynx to Isle Royale include:

- Plan the release of the animals during the ascending phase of the hare cycle. We recommend reintroducing lynx during the ascending phase of the cycle (Licht et al. accepted). The next ascending phase should occur around the year 2018-21. However, lynx might be more available during population peaks in Canada so there may be logistical advantages to planning a reintroduction 2021-23. Within a year the most optimum time for release appears to be during the spring snow melt (Devineau et al. 2011).

- Get the source animals from Ontario. Although using source animals from across North America may appear beneficial by increasing genetic diversity, lynx show little genetic variation or sub-structure throughout their range (Schwartz et al. 2002, Row et al. 2012). As a result, we recommend using source animals from nearby sites, as advised by Jamieson and

Lacy (2012) for species that show little genetic variation. Lynx from southwestern Ontario should readily adapt to Isle Royale, should be less costly to procure, and using such animals is consistent with NPS reintroduction policies (National Park Service 2006). However, there should be an attempt to avoid releasing kin and closely related animals. This would delay the onset of inbreeding impacts to the island population. Animals should be captured in winter using designs such as the one described by Kolbe et al. (2003).

- Release about 20 animals. Licht et al. (accepted) found that the probability of reintroduction success varied little between initial population sizes of 20 to 50. We recommend an initial release of about 20 lynx. Additional translocation resources are better spent on future supplementations than they are on increasing original population size.

- Conduct prescribed burns to increase hare habitat. Prescribed burns should be conducted in mature deciduous stands in an effort to return the stands to early seral stages. Burdett et al. (2007) found that snowshoe hare and lynx in Minnesota were most strongly associated with 10-30-year-old regenerating forests. The burns should be distributed in a way to provide a mosaic of successional stages across the park (Burdett et al. 2007). Although a lynx reintroduction could proceed without such an action, enhancing the habitat would enhance the likelihood of reintroduction success.

- Conduct a research and monitoring program. Due to the many uncertainties regarding the project, and the scarcity of scientific information regarding lynx ecology in areas devoid of anthropogenic impacts, the reintroduced animals should be monitored and managed using adaptive management principles. Released animals should be monitored using radio-telemetry equipment (preferably with GPS capability) to determine lynx survival, movements, recruitment, and other life history information. Ideally, this would be done through one complete 10-year cycle. At a minimum lynx would be monitored for a couple generations. Hare abundance should be monitored annually using pellet surveys (McCann et al. 2007).

- Consider supplemental releases if inbreeding or population persistence becomes a concern. Historically, lynx on Isle Royale might have constituted a meta-population that was periodically augmented and sustained with new animals from the mainland. The new animals brought genetic diversity to the island population. However, such immigration might no longer be possible due in part to global warming and the reduced frequency of ice-bridges forming between the island and the mainland (Licht et al. 2015). Yet, rather than adhere to a fixed augmentation schedule we recommend and adaptive management approach as natural immigration might still occur during the infrequent periods when an ice-bridge does form or inbreeding depression might be less of a concern than predicted in the simulations.

Potential Impacts

The following discussion highlights some potential impacts, both positive and negative, from a lynx reintroduction. This discussion primarily focuses on management and ecological impacts. A more thorough list of impacts (e.g., socioeconomics) and possible mitigating actions would need to be developed in a lynx reintroduction plan/environmental compliance document.

- A reintroduction would comply with National Park Service policies. The best available evidence indicates that lynx that were extirpated due to human actions and that a lynx reintroduction is likely to be successful, especially if accompanied with appropriate management. Although some might view a population as non-viable if anthropogenic supplementation is needed, we believe that in the case of Isle Royale lynx such supplementation can be justified as mitigation for climate change.

- A reintroduction would comply with the Endangered Species Act. The Canada lynx is listed as a threatened species in the contiguous 48 states. The Endangered Species Act directs all agencies to conserve listed species. Any reintroduction would require consultation with the U.S. Fish and Wildlife Service.

- A reintroduction of lynx to Isle Royale would provide a unique opportunity to study lynx ecology. As demonstrated by the long-running Isle Royale wolf-moose study, the island provides a unique laboratory to study wildlife and ecological processes (Schlesinger et al. 2009). In the case of lynx the animals would be reintroduced to an area with few anthropogenic impacts and threats compared to mainland sites (e.g., poaching, vehicle-caused mortalities). Furthermore, predators and competitors of lynx such as the coyote and bobcat are absent. The results from a lynx reintroduction to Isle Royale would greatly increase our understanding of lynx ecology and conservation.

- Lynx could compete with red fox. Lynx would likely compete with red fox for prey and resources. The degree and results of the competition is unknown, although there are records of lynx killing red fox (Stephenson et al. 1991, Sunde et al. 1999). Red fox appear to have first arrived on Isle Royale around 1925 (Cochrane 2013). It's unclear how they got to the island.

- Lynx could compete with marten. Marten appear to be indigenous Isle Royale with the island population genetically distinct from the mainland population (Romanski and Belant 2008, Romanski and Belant, unpub. data). Lynx and marten are competitors for food including snowshoe hare and red squirrel. There would likely be some competition on Isle Royale. However, both species appear to have historically co-existed on the island. To insure the health and viability of both populations a marten monitoring program should be considered as part of a lynx reintroduction program.

- Lynx, wolves, and moose would interact; however, the impacts should be negligible. There is no reason to believe that population-level impacts would occur between the three species. In very rare cases wolves could cause isolated incidents of lynx mortality. Conversely, lynx could benefit from wolf-killed moose carrion.

- Visitor experience would be enhanced by knowing lynx are present. Canada lynx are generally shy, secretive, and exist at low densities, and Isle Royale gets few backcountry visitors, so lynx observations might be rare (however, the number of sightings in the Colorado reintroduction are "quite high," R. Kahn, pers. comm., so observations could be more than anticipated). Even if observations are rare, visitor experience would be enhanced simply by knowing lynx are present. It is unlikely that the reintroduction of lynx would result in any management changes regarding visitor use or activities at the island.

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NPS 139/133624, August 2016

National Park Service
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